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The Biological Characteristics, Ecological Role and Evolutionary Significance of *Dickinsonia* and Other Modular Organisms of the Ediacara Biota

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by

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The text of this dissertation, in part or in full, is a reprint of the material as it appears in “Highly regulated growth and development of the Ediacara macrofossil *Dickinsonia costata”* (*PLoS ONE,* 2017, v. 12, e0176874); “You can get anything you want from Alice's Restaurant Bed: exceptional preservation and an unusual fossil assemblage from a newly excavated bed (Ediacara Member, Nilpena, South Australia)” (*Australian Journal of Earth Sciences,* 2019, doi: 10.1080/08120099.2018.1470110); “Slime travelers: early evidence of animal mobility and feeding in an organic mat world” (*Geobiology*, 2019, doi: 10.1111/gbi.12351). The co-author, Dr. Mary Droser, listed in that publication directed and supervised the research which forms the basis for this dissertation.

ABSTRACT OF THE DISSERTATION

The Biological Characteristics, Ecological Role and Evolutionary Significance of *Dickinsonia* and Other Modular Organisms of the Ediacara Biota

by

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The earliest fossil communities of macroscopic organisms are preserved in the Ediacara Biota. While many are difficult to classify into well-known phylogenetic groups, the exceptional preservation of these mostly soft-bodied forms, provides a plethora of material for comprehensive investigations of their biology and ecology. Exceptional deposits of the Ediacara Member from the Flinders Ranges and surrounding areas of South Australia yield abundant Ediacara Biota fossils ideal for such studies. The research presented below targets modular Ediacaran taxa, in particular the iconic and abundant fossil *Dickinsonia*. Patterns of growth and development in *Dickinsonia* are explained most parsimoniously via posterior addition of modular units and variable growth rates of units through development regulated to maintain an ovoid shape. Fossiliferous Ediacaran bedding plane surfaces, including the recently uncovered Alice's Restaurant bed, highlight the

heterogeneous distribution of taxa on the Ediacaran seafloor. Trace fossil evidence demonstrates that *Dickinsonia* and *Yorgia* were mobile, muscular organisms that fed on the organic mat through their ventral surface. Comparisons with other bilaterally symmetrical modular taxa suggests that many Ediacaran forms may have been mobile but did not engage in activities conducive to trace fossil preservation. *Dickinsonia* was bilaterally symmetrical, marked by distinct anterior/posterior and likely dorsal/ventral differentiation in addition to modules that met precisely at the midline. Taphonomic variants of *Dickinsonia* reveal that it was structurally resilient for a soft-bodied organism, highly extensible compared with most modern biopolymers, capable of elastic and plastic deformation, and composed of relatively thick, differentiated tissue. While many of these characters are consistent with bilaterians today this fossil probably represents an extinct clade within the Eumetazoa. This work establishes that the physiology and morphology of *Dickinsonia* were specifically suited to Ediacaran environments, and that departures from those unique conditions may have led to the ultimate disappearance of this taxa.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

LIST OF TABLES

CHAPTER 1

INTRODUCTION

The Ediacara Biota (571-542 Ma) preserves the oldest macroscopic, multicellular community-forming organisms in the fossil record (Xiao and Laflamme, 2009; Droser and Gehling, 2015). These largely soft-bodied taxa predate well-known Cambrian forms by more than 30 million years and there is general agreement that among them were stem-group members of the major animal clades, including sponges, ctenophores, cnidarians and bilaterians (Droser and Gehling, 2008; 2015; Zhu et al., 2008; Love et al., 2009; Clites et al., 2011; Erwin et al., 2011; Gehling et al., 2014; Gold et al., 2015; Droser et al., 2017). Assigning individual Ediacara Biota taxa to specific metazoan groups has traditionally proved contentious and, thus, establishing evolutionary relationships between fossils of the Ediacaran and Phanerozoic remains difficult (e.g. Xiao and Laflamme, 2009; Erwin et al. 2011). Studies of modern organisms provide predictive information about the potential morphology and phylogeny of the first complex, macroscopic animals on Earth. However, the fossil record offers the only means to test these predictions, to determine the biology and ecology of the organisms that composed these seminal communities, and to reconstruct the environmental context in which they evolved.

Traditionally, studies have “shoehorned” Ediacara Biota taxa into established phylogenetic groups, often based on qualitative observations derived from a

limited number of specimens (e.g. Sprigg, 1949). Instead, recent investigations employing novel techniques, independent of taxonomy, have yielded promising results highlighting patterns of growth and development, community and environmental interactions, as well as the various life modes and feeding habits present at the dawn of animal life (Laflamme and Narbonne, 2009; Tarhan et al., 2010; Zakrevakaya, 2014; Hoyal-Cuthill and Conway Morris, 2014; Hall et al., 2015; 2018; Mitchell et al., 2015; Rahman et al., 2015; Coutts et al., 2017; Darroch et al., 2017; 2019; Patterson et al., 2017; Reid et al., 2018; Droser et al., 2019b). A more quantitative approach applied to a significant number of specimens is necessary to decipher the biological and ecological characters of these early, complex forms and evaluate their place in the history of life on Earth.

Dickinsoniomorpha, an informal group of modular taxa with distinct anterior/posterior differentiation (Erwin et al., 2011; Laflamme et al., 2013), have proved particularly difficult to constrain despite a wealth of research, especially on the namesake *Dickinsonia*. Known from both the White Sea region of Russia and the Flinders Ranges and surrounding areas of South Australia, *Dickinsonia* was relatively abundant and one of the largest of the Ediacara Biota taxa, reaching sizes greater than 80 cm in total length (Sprigg, 1949; Jenkins, 1992; Gehling and Droser, 2013; Zakrevskaya, 2014). It is unique amongst the Ediacara Biota in that there are multiple recognized species of *Dickinsonia* (Sprigg, 1949; Glaessner and Wade, 1966; Wade, 1972; Keller and Fedonkin,

1977; Jenkins, 1992), although the current number may be inflated (Zakrevskaya and Ivantsov, 2017). It is thought to have been bilaterally symmetrical and capable of movement (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010), however both of these characters have been questioned in recent literature (Ivantsov, 2007; Retallack et al., 2007; McIlroy et al., 2009; Budd and Jensen, 2017).

Interpretations of the phylogenetic placement of *Dickinsonia* have varied dramatically, and include assignments to annelids (Wade, 1972), fungi or lichen (Retallack, 2007), protists (Seilacher et al., 2003), ctenophores (Zhang and Reitner, 2006), placozoans (Sperling and Vinther, 2010) and even an extinct kingdom (Seilacher, 1992). Recent studies, including the chapters presented below, suggest that it possessed eumetazoan grade body organization (Gold et al., 2015; Hoekzema et al., 2017; Bobrovskiy et al., 2018; 2019). As one of the more complex and recognizable taxa of the Ediacara Biota, it provides potentially critical insight into our understanding of the evolution of early animals.

Results presented here are based on the examination of 1,353 body fossils and 130 trace fossils of *Dickinsonia* from the Ediacara Member, South Australia, as well as hundreds of other modular, bilaterally symmetrical taxa and thousands of Ediacaran fossil organisms. The Ediacara Member is well exposed in the Flinders Ranges and surrounding areas (Figure 1; Gehling, 2000). Thousands of

specimens from this region are housed at the South Australia Museum in Adelaide (identified with P numbers). Additional research was conducted at the National Heritage Nilpena Station field site, where excavation of 35 bedding planes (identified by the bed on which they are preserved) yields hundreds of square meters of *in situ* fossiliferous material (Droser et al., 2019a).

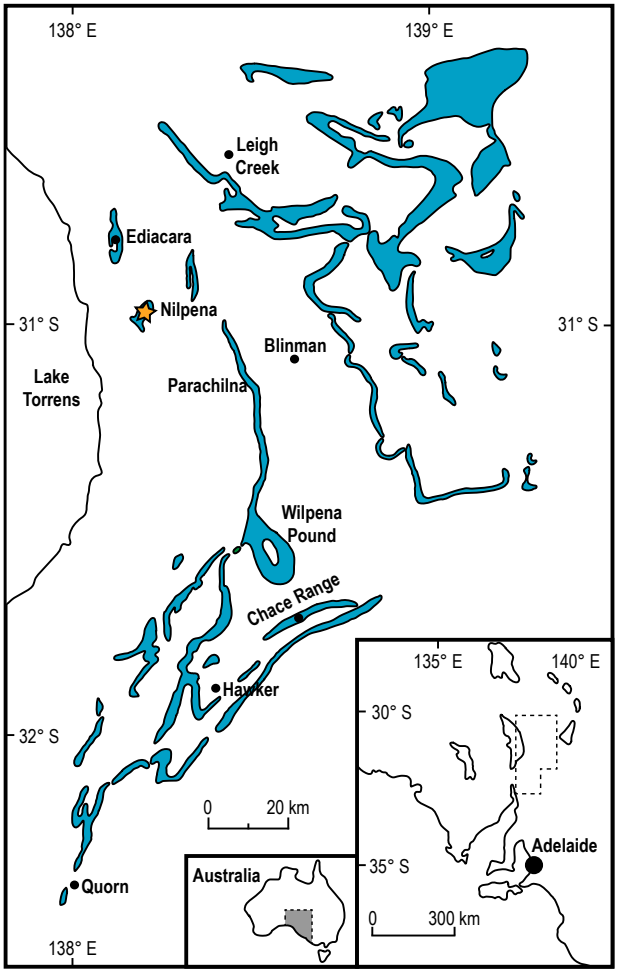

Figure 1. Map of the Flinders Ranges with outcrops of the Ediacara Member in blue and the National Heritage Nilpean station field site identified by the yellow star. Edited from Gehling and Droser, 2009.

The goal of this dissertation is to investigate the biology and ecology of modular, bilaterally symmetrical Ediacaran taxa, with specific emphasis on abundant *Dickinsonia* from the Ediacara Member. It begins with a quantitative assessment of the growth and development of *Dickinsonia.* This is followed by a description of the unique bedding plane surface, Alice's Restaurant Bed, uncovered in 2017, targeted for exceptional preservation of *Dickinsonia* and two rare dickinsoniomorphs: *Andiva* and *Yorgia*. Results presented here and in the following chapter document evidence of mobility in the Ediacara Biota, with Chapter 3 focused on investigations of *Dickinsonia* and associated trace fossils. The final chapter details the biomechanical properties of *Dickinsonia* based on investigations of specimens from a variety of taphonomic settings. Together, these studies provide a comprehensive view of the relative complexity of *Dickinsonia* and related organisms and demonstrates that they were uniquely adapted to Ediacaran environments.

CHAPTER 1. HIGHLY REGULATED GROWTH AND DEVELOPMENT OF THE EDIACARA MACROFOSSIL *DICKINSONIA COSTATA*

Abstract

The Ediacara Biota represents the oldest fossil evidence for the appearance of animals but linking these taxa to specific clades has proved challenging. *Dickinsonia* is an abundant, apparently bilaterally symmetrical Ediacara fossil with uncertain affinities. We identified and measured key morphological features of over 900 specimens of *Dickinsonia costata* from the Ediacara Member, South Australia to characterize patterns in growth and morphology. Here we show that development in *Dickinsonia costata* was surprisingly highly regulated to maintain an ovoid shape via terminal addition and the predictable expansion of modules. This result, along with other characters found in *Dickinsonia* suggests that it does not belong within known animal groups, but that it utilized some of the developmental gene networks of bilaterians, a result predicted by gene sequencing of basal metazoans but previously unidentified in the fossil record. *Dickinsonia* thus represents an extinct clade located between sponges and the last common ancestor of Protostomes and Deuterostomes, and likely belongs within the Eumetazoa.

Introduction

The Ediacara Biota is generally accepted as the first occurrence of macroscopic, complex, animals in the fossil record (Xiao and Laflamme, 2009; Droser and Gehling, 2015). Predictions based on gene sequencing of basal metazoans suggest that within these early communities, in addition to ancestral animal forms, we should find extinct lineages that do not fit within known animal phyla (Erwin, 2009). Despite this, previous attempts to classify Ediacara fossils have focused on placing them within extant animal clades and thus have proved unsuccessful, leaving significant gaps in our understanding of early animal evolution. Recent work focused on determining relationships within the Ediacara biota based on morphological similarity has demonstrated the utility of interpreting characters of these organisms independent of previously recognized phylogenetic schemes (Xiao and Laflamme, 2009; Laflamme et al., 2013). *Dickinsonia* is an abundant member of the Ediacara Biota that was mobile and seemingly complex (Gehling et al., 2005). Despite numerous interpretations (Sprigg, 1949; Seilacher, 1992; Seilacher, 2003), from fungi (Retallack, 2007) to annelids (Wade, 1972; Runnegar, 1982), and recently to placozoans (Sperling and Vinther, 2010) and bilaterians (Gold et al., 2015), the phylogenetic placement of *Dickinsonia* remains controversial (Budd and Jensen, 2017).

Specimens of *Dickinsonia* occur in the Ediacara Member of the Rawnsley Quartzite, cropping out in the Flinders Ranges and surrounding areas of South

Australia (Figure 1). Ediacara Member fossils are preserved in sandstones characterized by episodic deposition (Gehling, 1999; Gehling and Droser, 2013). Early mineralization of these deposits after burial yields exceptional preservation of organisms such as *Dickinsonia* as external molds in negative relief on the bases of beds (Gehling, 1999; Tarhan et al., 2016). The majority of specimens are in excellent condition indicative of *in situ* preservation. However, *Dickinsonia* is found in a range of preservational modes, including folded, ripped and clearly transported individuals, and some with evidence of death prior to burial (Gehling and Droser, 2013; Evans et al., 2015). These factors make it critical that an abundance of specimens be examined to eliminate taphonomic processes as a cause of morphologic variability.

In the Ediacara Member *Dickinsonia costata* is the most abundant of the five currently recognized species of *Dickinsonia*. Current species distinctions are based largely on overall shape and size as well as the size of modules (Sprigg, 1949; Wade, 1972; Glaessner and Wade, 1977; Jenkins, 1992). Compared to other species *D. costata* is ovoid in shape and has the fewest number of modules per unit length. We use the terms anterior and posterior (see Figure 2 for all morphological characters) as defined by the inferred direction of movement (Gehling et al., 2005). *Dickinsonia* contains a midline running parallel to the long axis of the body and is divided into numerous repeated features that have been variously referred to as segments (Geling et al., 2005; Retallack, 2007; Wade,

1972) or modules (Sperling and Vinther, 2010; Evans et al., 2015). Segments are conservatively defined as repeated units along the anterior-posterior axis containing anterior-posterior polarity within individual units (Hannibal and Patel, 2013). No such polarity within units has been recognized for *Dickinsonia*, so we refer to them as modules following previous authors (Sperling and Vinther, 2010; Evans et al., 2015). Modules are smallest at the posterior end (Gehling et al., 2005, Runnegar, 1982; Sperling and Vinther, 2010; Gold et al., 2013; Budd and Jensen., 2017). The anterior most unit is distinct from other modules in that it is not divided by the midline. All modules, as well as the anterior most unit, terminate at a smooth, well-defined outer margin. Length refers to any feature that for the majority of modules is approximately parallel to the long axis of a specimen and width is parallel to the short axis.

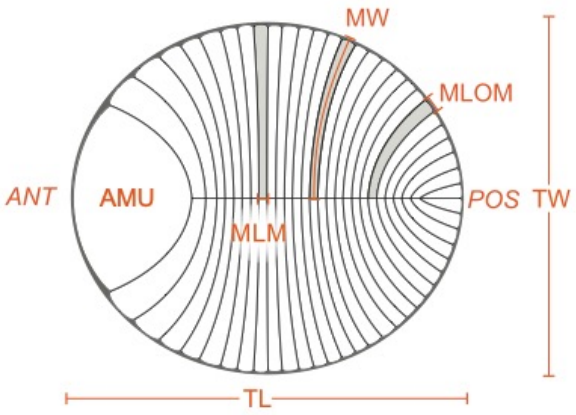

Figure 2. Illustration of representative *Dickinsonia costata.* Labels represent posterior (POS), anterior (ANT), total length (TL) and width (TW), module length at outer margin (MLOM) and midline (MLM), module width (MW) and anterior most unit (AMU). Illustration by Sohail Wasif.

Previous descriptions of *Dickinsonia,* relying on relatively few specimens, have presented conflicting views on morphology (Fedonkin, 2003; Gehling et al., 2005; Ivantsov, 2007; Brasier and Antcliffe, 2008; Dzik and Ivantsov, 2002; Dzik, 2003; Zhang and Reitner, 2006; Dzik and Martyshyn, 2015; Gold et al., 2015; Budd and Jensen, 2017). Some authors have suggested that the modules of *Dickinsonia* were offset at the midline, invoking a glide plane of symmetry (Fedonkin, 2003; Ivantsov, 2007; Brasier and Antcliffe, 2008), others contend that modules run continuously through the midline and that the organism was bilaterally symmetrical (Gehling et al., 2005; Gold et al., 2015), and some have claimed that both forms are present (Budd and Jensen, 2017). Further, it has recently been suggested that the modules of *Dickinsonia* bifurcated, merged and changed in relief (Braiser and Antcliffe, 2008). Other reports have suggested that *Dickinsonia* possessed complex internal structures (Dzik and Ivantsov, 2002; Dzik, 2003; Zhang and Reitner, 2006; Dzik and Martyshyn, 2015).

Here we present analyses of a significant number of specimens to refine the morphology of *D. costata.* In addition, we collected measurements of key morphological characters that chronicle the growth and development of this organism to determine how it fits in the early evolution of animal life. Our results indicate that *Dickinsonia* represents a previously unrecognized lineage of eumetazoans that utilized some of the gene regulatory networks found in

bilaterians and likely went extinct prior to the rise of more recognizable animal forms during the Cambrian.

Materials and methods

We photographed, documented and observed morphologic variation in 988 specimens of *D. costata* from the South Australia Museum (SAM) in Adelaide and Nilpena, a field site west of the Flinders Ranges, South Australia. The Nilpena site is a privately owned property and permission to conduct this research was granted via the landowners Ross and Jane Fargher (see acknowledgements). Ongoing excavation at Nilpena over the last 15 years has resulted in the exhumation of 28 beds and over 300 m^2 of *in situ* fossiliferous material (see Joel et al., 2014 for further description of bed excavation). All figured specimens are either deposited at the SAM (P53893, P41202 and P41074) where they are publicly accessible, or, in the case of specimens from Nilpena (1TFB-01 and MM3-01), are preserved on *in situ* bedding planes and cannot be removed from the site.

Of the 988 total specimens examined here, length and width were measured from 538 complete specimens with no evidence of deformation using digital calipers on original specimens or latex molds. The number of modules was counted directly from fossil specimens preserved well enough to consistently identify discrete modules. This process yielded 194 specimens for which we

could accurately determine module numbers. Reported module numbers necessarily represent minimum estimates as modules near the posterior end of many specimens become smaller than the resolution of the grains in which they are preserved. Simple linear regression models were conducted using the Minitab® Statistical Software and p-values are reported for F- (analysis of variance or ANOVA) and t-tests.

Module length at the midline and outer edge as well as module width were measured on the 94 best preserved specimens using photographs and the Image J software available at https://imagej.nih.gov/ij/. These specimens were chosen based on the ability to measure individual module features for a significant (>75%) portion of the specimens total modules. Module lengths were measured as straight-line distances at the midline and outer edge. Module width was measured along the sinusoidal path of the module from midline to outer edge. For Figures 4 and 5 we chose five representative samples (Figure 3) that accurately summarize the findings of this analysis (see Figure 4 and 5 for the same analysis on 5 additional specimens). We calculated the average increase in module length at the outer margin as the sum of the outer margin module length on the right and on the left side for each module, minus the sum of these lengths for the module located immediately posterior, divided by the sum of the module length at the outer margin for the module. Measurements of length and width were obtained from the anterior most unit and compared to the sum of the

module lengths at the outer margin for the right and left side of the first anterior module.

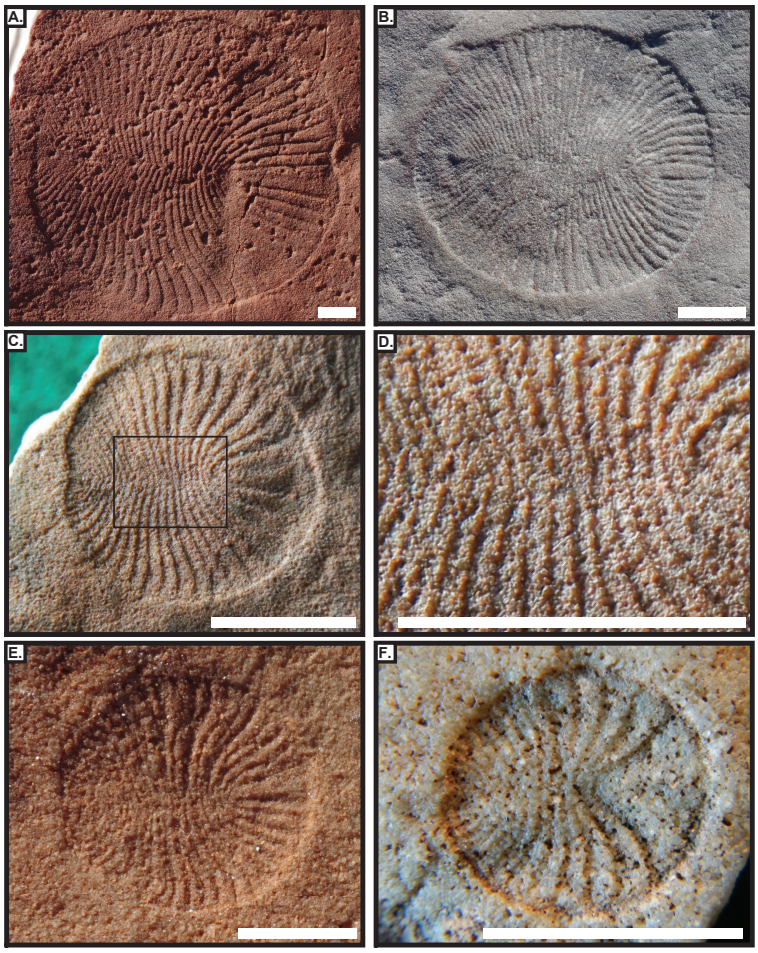

Figure 3. Representative fossil specimens of *D. costata.* Specimens from the Ediacara Member, Rawnsley Quartzite used to demonstrate growth patterns in Figs 4 and 5. Notice the clear bilateral symmetry and smooth, well-defined outer margin in all specimens. The box in panel C represents the zoomed in area shown in panel D. (A) SAM P53893. (B) 1TFB-01. (C,D) SAM P41202. (E) MM3-01. (F) SAM P41074.

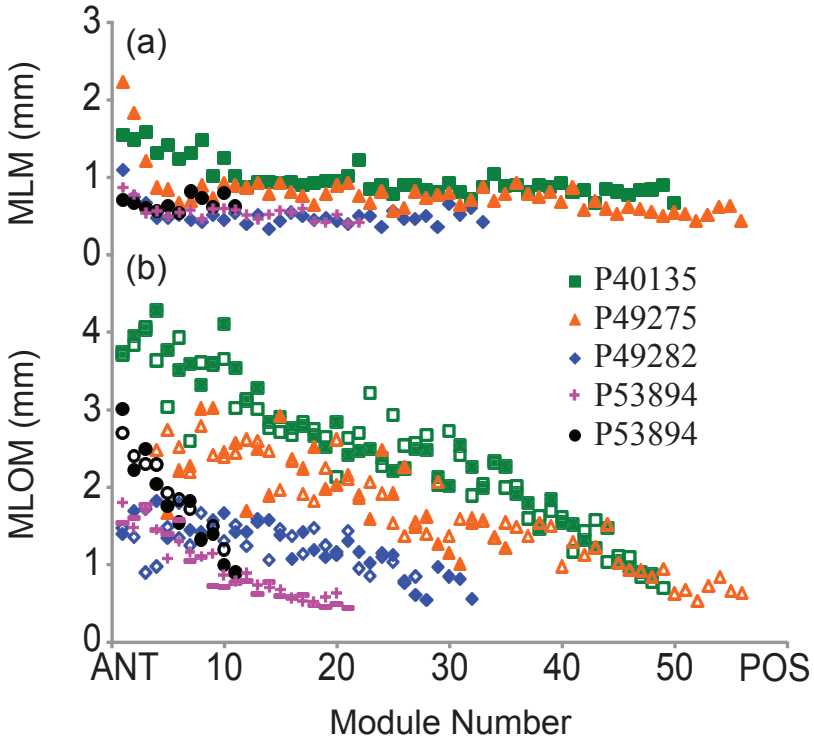

Figure 4. Graphical representation of (a) module lengths along the midline (MLM), and (b) module lengths along the outer margin (MLOM) versus number of modules for five illustrative specimens of *D. costata*. Moving from anterior (ANT) to posterior (POS) from left to right along the x-axis. Open and closed shapes in (b) represent opposite sides of the same specimen.

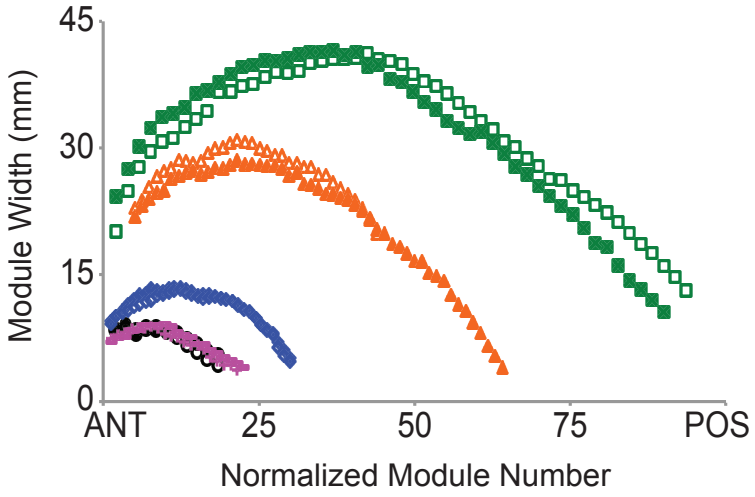

Figure 5. Module width (MW) versus normalized module number for *D. costata*. Moving from anterior (ANT) to posterior (POS) from left to right along the x-axis. Shapes and colors represent the same specimens from S2 Fig. Module number is normalized to total length by dividing the module number by the total number of modules and multiplying by total length. Open and closed shapes represent opposite sides of the same specimen.

Results and discussion

Morphological observations

This investigation of over 900 specimens of *D. costata* represents the largest dataset of this taxon analyzed to date, thus illuminating which features are representative of organismal biology and those that represent taphonomic artifacts. The shape of *D. costata* is consistently ovoid in all specimens investigated except in rare examples that have obviously been altered by

taphonomic processes. The best-preserved specimens of *D. costata* clearly show that modules are continuous across the midline (Figure 3D). It is highly unlikely that this precise matching is caused by distortion, suggesting that this organism was bilaterally symmetrical. Further, close examination demonstrates that any apparent evidence for modules being offset at the midline is the result of alteration due to the soft-bodied nature of *Dickinsonia* and that modules are consistently symmetric about the long axis in all specimens. This indicates that previously reported evidence for offset modules (Fedonkin, 2003; Ivantsov, 2007; Brasier and Antcliffe, 2008) is likely the result of taphonomic distortion, which is probable given the variable preservation of *Dickinsonia*, or could reflect a previously unrecognized species distinction between specimens from South Australia, with bilateral symmetry, and those with reported offset symmetry from elsewhere. There is no evidence that modules bifurcate or merge in a biologically meaningful way and all modules in body fossils of *D. costata* are preserved in varying degrees of negative relief. While individual specimens may appear to have these features, their occurrence is rare and can be attributed to taphonomic deformation. No evidence for internal structures was observed in any specimens analyzed herein. All previous reports of features such as a through gut are likely due to deformation or the draping of *Dickinsonia* over irregular features present on the Ediacaran seafloor.

Overall growth

Measurements of total length for *D. costata* range from 4.15 to 140.55 mm with a mean value of 24.31 mm and total width ranges from 3.38 to 130.11 mm with a mean value of 21.06 mm. The relationship between overall length and width is strongly linear ($R^2 = 0.98$) and through the origin (Figure 6A). Linear regression models support a statistically significant correlation between total length and width ($p < 0.0001$ for both F- and t-tests). Height is not easily resolved from specimens of *Dickinsonia* and fluctuations in height are not singularly controlled by biological factors due to compaction and taphonomic variability. There is no evidence to suggest that taphonomic effects are size dependent and changes in height are insignificant with respect to length and width. Typically, the preserved height of *D. costata* is less than 1 to 2 mm and rarely greater than 5 mm in total relief. These results are consistent with previous examinations of this species (Sprigg, 1949; Runnegar, 1982; Retallack, 2007).

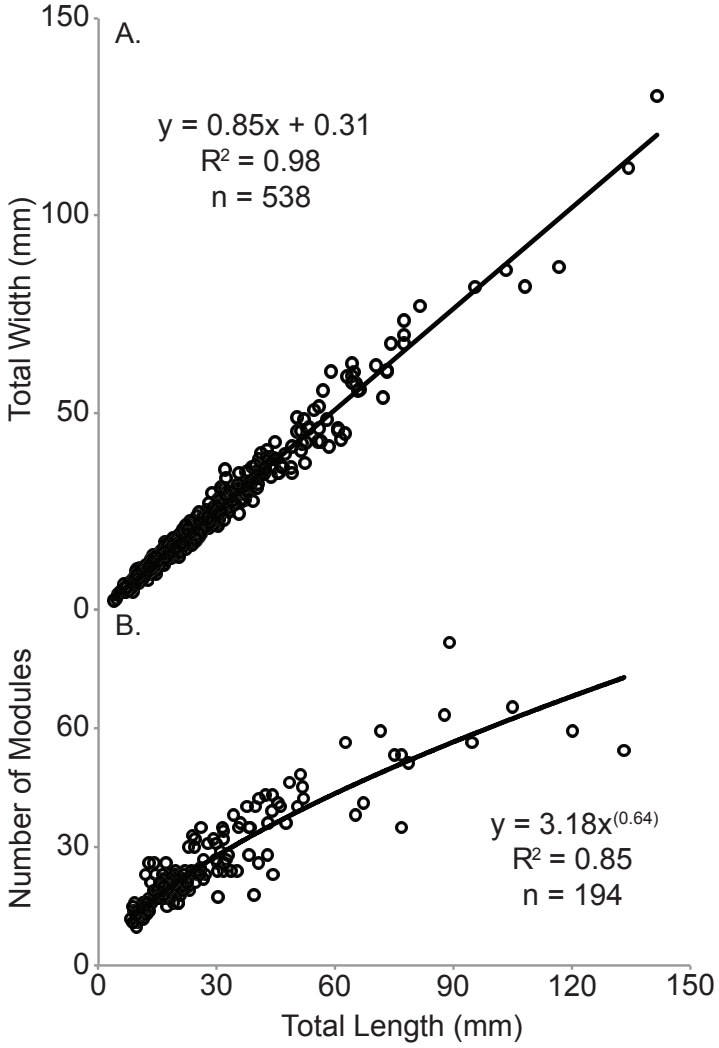

Figure 6. Graphical representation of overall growth. (A) Total width, and (B) number of modules versus total length of *D. costata* with best-fit line plotted, equation and R^2 of best-fit as well as total number of specimens (n).

Our data are in agreement with previous reports (Sprigg, 1949; Runnegar, 1982; Retallack, 2007) suggesting isometric growth of *D. costata* in terms of total length and width. This result is especially striking when we consider the soft-bodied

nature of this organism. The linear trend indicates that overall length and width increased throughout the life of *D. costata* and that the co-variation between these metrics represents one of the strongest constraints on growth. The consistency of the length to width relationship, as well as the lack of significant variation with respect to height, indicates that maximizing the surface area to volume ratio was an important factor in the development of *D. costata* (Runnegar, 1982). Maintaining a consistent length to width ratio also likely contributed to the conservation of an overall ovoid shape.

There is a moderate ($R^2 = 0.77$) positive linear relationship between total length and number of modules, however a power function yields a slightly stronger trend ($R^2 = 0.85$; Figure 6B). Linear regression models support a statistically significant correlation between total length and number of modules ($p < 0.0001$ for both F- and t-tests). In general this positive relationship indicates that as *D. costata* grew the number of modules increased. The slightly better fit of a power law suggests that there may be an upper limit to the number of modules in *D. costata* and that the organism added fewer modules the larger it became.

Despite this moderate trend in module number relative to size, some individuals have up to three times as many modules as those with similar overall lengths. The inverse relation is also identified in specimens where length can be more than three times greater in one specimen than in another with a similar number of

modules. While these examples represent extreme end members of the overall distribution, it is common to find specimens with the same number of modules that vary in size by at least a factor of two. The variability in module number versus total length cannot be attributed to currently recognized species distinctions and the continuum of values in Figure 4B suggests that the plasticity of module numbers is not due to the presence of multiple unrecognized species. The inconsistency of module number with respect to size and the limited number of relatively large specimens prevent any definitive conclusions but suggest that module number and body size are only slightly correlated. Runnegar (1982) attributed this difference to the expansion and contraction of *Dickinsonia*. Observation of numerous variations within the general ovoid shape of this organism indicates that *D. costata* was likely capable of expansion and contraction. However, the three fold difference of module number in specimens with similar lengths and in total length in specimens with similar module numbers cannot be singularly explained by expansion and contraction, especially given the tightly constrained length to width ratio for this organism. End members of each example also do not consistently show evidence of expansion or contraction. We therefore conclude that the number of modules is not solely determined by overall size and that similarly sized specimens can have vastly different module numbers. The reasons for large differences in module number between specimens may simply be random as has been observed in the modern polychaete *Platynereis dumerilii* in which siblings living in close association have

been observed with vastly different numbers of segments (Fisher and Dorresteijn, 2004). This suggests that there was likely little functional significance in maintaining a specific number of modules with respect to size and highlights that conserving an ovoid shape and consistent length to width ratio was critical for *D. costata*.

Growth of modules

Comparison of module lengths at the midline and outer edge of *D. costata* demonstrates two distinct trends (Figure 7). Module lengths along the midline do not vary within an individual except at the anterior-most end where the first few modules are rarely much larger than subsequent modules (Figure 4). At the posterior, where new modules are added, module lengths similarly do not vary at the midline. There is a weak ($R^2 = 0.64$) positive correlation between average module lengths along the midline and total length indicating that at the midline, all module lengths increased uniformly with growth (Figure 8).

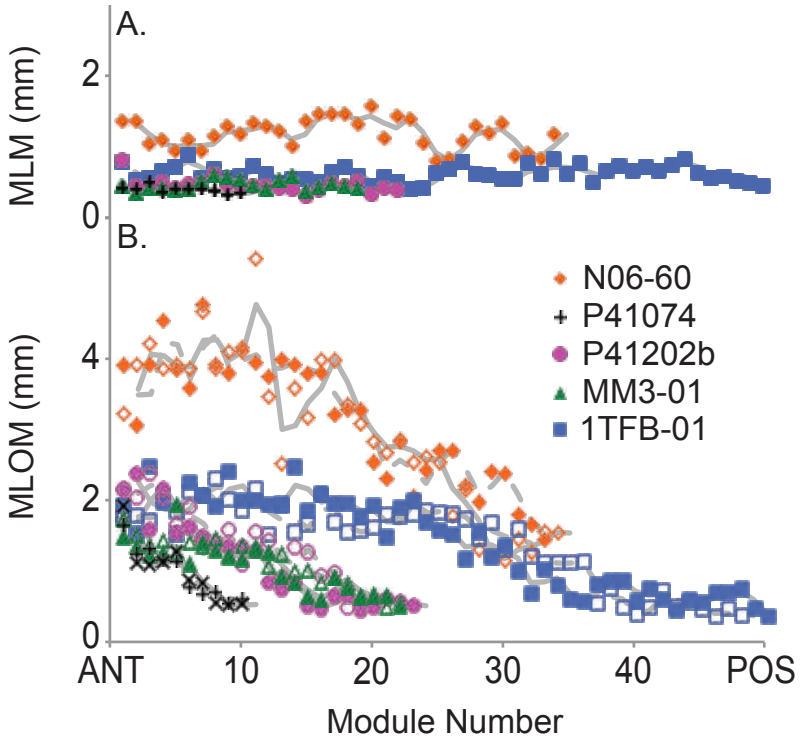

Figure 7. Graphical representation of changes in module length. (A) Module lengths along the midline (MLM), and (B) module lengths along the outer margin (MLOM) versus number of modules for five illustrative specimens of *D. costata*. Moving from anterior (ANT) to posterior (POS) from left to right on the x-axis. Grey trend lines represent two point moving averages. Open and closed shapes in (B) represent opposite sides of the same specimen, dotted trend lines correspond to open shapes.

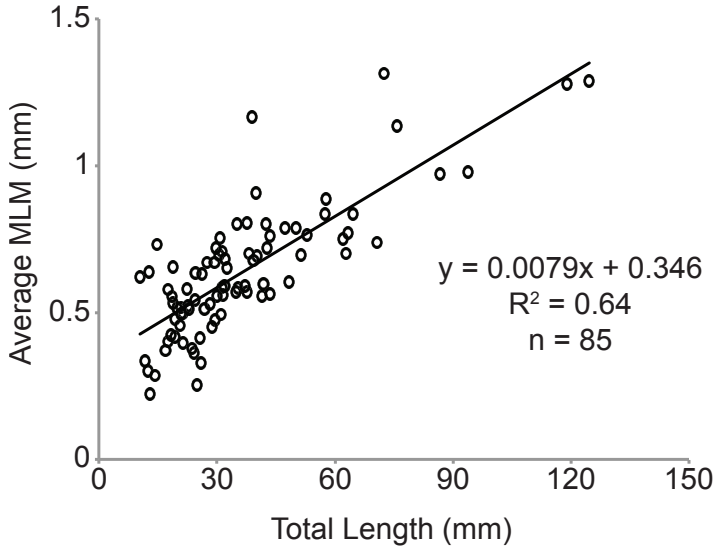

Figure 8. Graph demonstrating increase of the average module length at midline (MLM) as total length increases.

The consistency along the midline of *D. costata* suggests that module length increased rapidly when initially inserted to match previous modules at the midline. Once the length of an inserted module reached that of preceding modules at the midline, it grew at the same rate as all other modules, getting larger along with total length. The conservation of midline length is noteworthy given the irregularity of module numbers relative to overall size and suggests that, like total length and width, maintaining module length along the midline was a constraining factor in the growth of *D. costata*. The consistency of module lengths within individual specimens also indicates that modules were in some way fixed at the midline.

Module lengths at the outer margin decrease from anterior to posterior regardless of specimen size (Figure 7B). This suggests that the length of individual modules at the outer margin expanded consistently through life. Typically module lengths at the outer margin increase with total length linearly. The average increase in module length from adjacent modules at the outer margin is 4.01 $\pm$ 13.23% (SD). Measurements of the length at the outer margin for the anterior most unit show that in 29 out of the 94 best preserved specimens this feature is more than 20% larger, and in 13 specimens more than 50% larger than the sum of module length at the outer margin for the right and left side of the first true anterior module (e.g. Figure 3F).

Previous reports have suggested that *Dickinsonia* grew by the posterior addition of modules, based on the observation that modules are smallest at the posterior end (Gold et al., 2015). The lack of any branching modules or smaller intercalated modules in the hundreds of specimens analyzed indicates that they are not added between the posterior and anterior end by bifurcation of pre-existing modules. It is reasonable then to conclude that modules must either be added at the posterior or anterior end. Grain size limitation does not allow detailed examination of the posterior-most modules. However, the lack of any branching in the anterior-most module, which is large enough to be clearly seen in most specimens, suggests that modules are not released at the anterior end. The presence of specimens with the anterior most unit significantly larger than

the proceeding modules provides additional evidence that modules were not added at the anterior end. Thus, our data demonstrate that the most parsimonious explanation for module addition is that they were added at the posterior end.

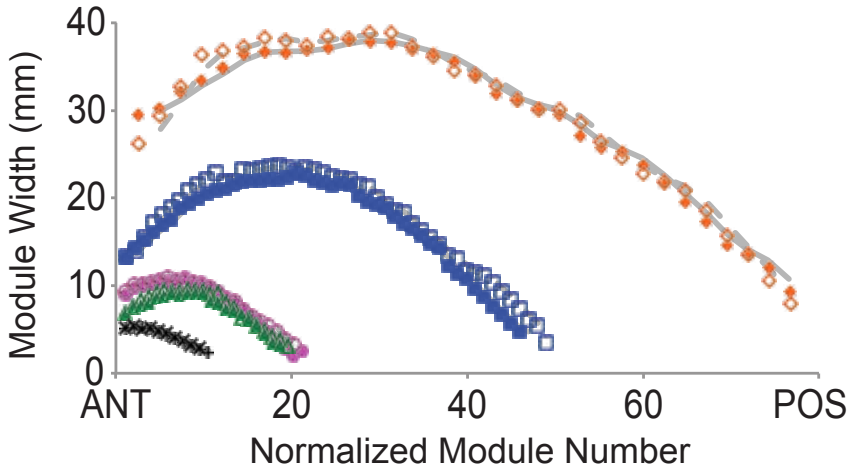

Figure 9. Graphical representation of changes in module width. Module width (MW) versus normalized module number for *D. costata*. Moving from anterior (ANT) to posterior (POS) from left to right on the x-axis. Grey trend lines represent two point moving averages. Shapes and colors represent the same specimens from Figure 7. Dotted trend lines correspond to open shapes. Module number is normalized to total length by dividing the module number by the total number of modules and multiplying by total length. Open and closed shapes represent opposite sides of the same specimen.

Dickinsonia costata module widths are smallest at the posterior end, increase up to roughly the middle of the long axis and then decrease towards the anterior end (Figure 9). Within specimens anterior-most modules are still larger than posterior-most modules. This indicates that while module widths increased through growth, a given module increased faster when it was at the posterior half of the organism. This trend is observed consistently in all specimens regardless of total length or module number.

The different growth rates for the characters discussed above result in variable module shapes both between specimens and within individual specimens of *D. costata* (Figure 10). In general though, posterior modules run straight from the midline to the outer edge at some angle less than 90 degrees forming a roughly "v" shape. From the posterior towards the middle of the long axis of a specimen this angle increases and becomes perpendicular to the midline. From this point to the anterior of a specimen modules typically bend so that they are still approximately perpendicular where they intersect the midline but become roughly parallel to the midline closer to the outer edge, forming "u" shaped modules. The soft-bodied nature of *D. costata* leads to many variations preserved within this approximate trend in module shape change. The "bending" of anterior modules indicates that modules must have been fixed not only at the midline, but also at the outer margin to some type of membrane. Increases in overall module size must have occurred in concert with the growth of this membrane. The variations

in module width and length at the outer margin from one side to another within even the most pristine specimens further suggest that this outer membrane must have been somewhat flexible, but rigid enough to regulate predictable changes in module shape.

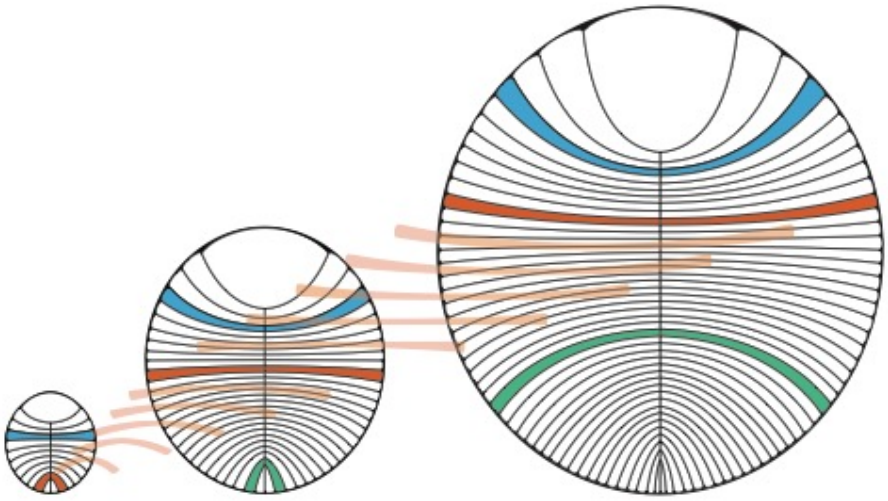

Figure 10. Idealized cartoon of *D. costata* growth. Illustration demonstrating the changes that occur in module shape and size with increases in total length and width. Illustration by Sohail Wasif.

The observed variations in module size, growth rate and shape appear to reflect the importance of maintaining the characteristic ovoid shape of *D. costata* while accommodating growth. Modules grew longer at the outer margin and wider to increase the size of the organism. Variable growth patterns of module widths and changes in module shape were adjusted during growth to maintain an ovoid

morphology (similar to the parabolic description of segments by Runnegar, 1982). This constrained growth pattern likely occurred in association with, or as a consequence of a tough yet pliable outer membrane. Our data demonstrate that despite an apparently simplistic morphology, *D. costata* modules grew by terminal addition and module inflation in a highly regulated and complex manner.

Comparison with other taxa

Other Ediacaran organisms, such as *Charnia,* grew by the addition and inflation of modular body divisions to achieve relatively large sizes (Antcliffe and Brasier, 2007). These Rangeomorph taxa grew by the repetition and branching of self-similar units, creating the characteristic fractal body pattern and achieving maximum surface area by 3D space filling (Hoyal Cuthill and Conway Morris, 2014). In contrast, *D. costata* grew to maximize 2D space, surface area to volume ratios, and all aspects of module inflation were regulated to maintain an ovoid shape. This suggests that rather than close phylogenetic relation between these two groups, that the addition and inflation of modular units was a common growth strategy and that the underlying regulatory genes that produce this style of growth may be present in a diversity of disparate forms within the Ediacara Biota. This result also demonstrates that there were diverse growth strategies in which modular Ediacaran organisms could maximize surface area, particularly while attaining large body size.

A natural comparison arises between the growth of segmented animals (annelids, arthropods and vertebrates) and *D. costata*. There are many obvious differences between these groups beyond the definition of a true segment discussed above, for instance all truly segmented animals have a trunk composed of segments that is distinct from the head and tail (Hannibal and Patel, 2013). Further, while there is a wide range of growth patterns found in the diverse array of known segmented organisms, those patterns typically follow specific rules. For example, arthropods grow by molting, and many arthropods have a constant growth rate per-molt, the so-called Dyar's rule (Klingenberg and Zimmermann, 1992). Because segment addition occurs in association with molting, size and number of segments, as well as the number of molts and thus age, are strongly correlated (Fusco et al., 2004; 2011). The plasticity of module number with respect to overall size between specimens of *D. costata,* despite the tight regulation on modular growth, suggests that module number is not a reliable proxy for age and that different specimens add and inflate modules at variable rates. This suggests that growth in *Dickinsonia* is fundamentally different from that of truly segmented animals.

We are not currently aware of any modern or extinct organism, segmented or otherwise, that grows in the same manner as *D. costata.* Any convergence between the growth of *D. costata* and modern organisms would likely reflect the importance of maintaining an ovoid shape and not phylogenetic ancestry. This is

consistent with previous explanations for the morphological similarities between *D. costata* and modern organism that are most likely unrelated (Runnegar, 1982; Gold et al., 2015).

Dickinsonia was one of the few mobile Ediacara taxa (Gehling et al., 2005) and it possibly fed via external digestion of organic matter through its ventral surface, leading to the hypothesis that it may have been related to modern Placozoa (Sperling and Vinther, 2010). In terms of growth, *Trichoplax adhaerens*, the only known species of placozoan, is highly irregular, with increasing variability as size increases, and has even been reported to change from circular to elongate in successive generations of asexually reproducing populations (Pearse, 1989; Syed and Schierwater, 2002; Maruyama, 2004; Pearse and Voigt, 2007). Individuals can also change dramatically in terms of both shape and size without truly growing (Pearse, 1989). These large fluctuations are inconsistent with the tight constraint on overall body shape observed for *D. costata*. This result does not exclude a placozoan affinity for *D. costata,* but it highlights a major difference in growth between the two organisms. The large discrepancy in growth patterns between *Dickinsonia* and placozoans indicates that the overlapping characters between the two groups are more likely due to similarities in function rather than reflective of phylogenetic ancestry.

Phylogenetic placement

It is generally agreed that the split between bilaterians and other animals occurred prior to the evolution of *Dickinsonia* (Erwin et al., 2011). Fossils of bilaterians have been identified from the Ediacara biota; the furrowed trace fossil *Helminthoidichnites* is widely accepted as evidence of bilaterians and the body fossil *Kimberella* is largely accepted as a bilaterian and has been reconstructed as a stem group mollusk [Erwin, 2009; Erwin et al., 2011; Ivantsov, 2009 but see Budd and Jensen, 2014 for discussion]. The highly regulated growth of *Dickinsonia*, along with features such as posterior addition, bilateral symmetry and organization around an anterior-posterior axis are characteristics found in bilaterians. However, most bilaterians are triploblastic and have a through gut and there is no evidence for the number of tissue layers or the presence of a mouth, anus or any type of gut in *Dickinsonia*. Some highly derived modern bilaterians do not have a through gut (Gierre and Erséus, 2002) and many studies have demonstrated the importance of the secondary loss of characters in phylogenetic reconstructions (Jenner, 2004), but it is unlikely that *Dickinsonia* is highly derived and our results suggest that it does not have the suite of characters necessary to be considered a crown group bilaterian. The latest attempt to classify *Dickinsonia* allied it with bilaterians, either as part of the stem or crown group, based on the likelihood that growth by terminal addition did not extend beyond ancestral bilaterians in the animal tree (Gold et al., 2015). Recent phylogenetic analysis suggests that the ancestral bilaterian was an

unsegmented, benthic, ciliated, acoelomate that was likely meiofaunal and contained a “blind-gut” (Struck et al., 2014; Laumer et al., 2015; Cannon et al., 2015). *Dickinsonia* was very sturdy and our analysis suggests that it had an outer membrane, but there is no evidence as to the total number of tissue layers. It reached relatively large sizes, with *D. rex* known to be as large as 1 meter in total length. It was mobile, bilaterally symmetrical, and likely obtained nutrients though external ventral digestion (Gehling et al., 2005; Sperling and Vinther, 2010). It is modular but it is possible that this is not a precursor to, or otherwise homologous with, segmentation in bilaterian clades. The presence of features likely characteristic of more derived bilaterians, such as large body size, and lack of those thought to be present in the ancestral bilaterian, such as any type of gut, make the placement of *Dickinsonia* within the stem group unlikely. However, these characters are reliant on problematic ancestral state reconstructions (Halanych, 2015; Pisani et al., 2015) so the possibility of *Dickinsonia* as a precursor to bilaterians cannot be ruled out.

The discovery of developmental patterns in *D. costata* that were used to conserve an ovoid shape demonstrates that growth was complex and surprisingly well regulated. The unique set of features exhibited by *D. costata* supports the hypothesis proposed by Erwin and Davidson (2002) and corroborated by gene sequencing of basal metazoan (Erwin, 2009) that the gene regulatory networks needed to produce the complex morphologies of bilaterians

were present in more ancestral animals. In this hypothesis *Dickinsonia* would represent part of an extinct lineage that split somewhere between sponges and the LCA of Protostomes and Deuterostomes and took advantage of particular developmental gene networks common to cnidarians and higher-grade animals, but not all of those found in modern bilaterians (Erwin and Davidson, 2002; Erwin, 2009; Tweedt and Erwin, 2015). The relative complexity of growth along with the identification of an outer tissue layer, when considered with all other features of *D. costata,* further suggests that this lineage likely belongs within the Eumetazoa. Recent analysis has shown that microRNAs evolved independently multiple times, suggesting that convergence cannot be ruled out when considering relations based on morphological similarities (Robinson et al., 2013). While the available data is not sufficient to eliminate convergent evolution as a possible explanation for these shared characters, the number of similar traits that are related to the gene regulatory networks found in all animals suggest that the most parsimonious placement for *Dickinsonia* is as an extinct lineage of Eumetazoa.

Traditionally, taxa of the Ediacara Biota have either been shoehorned into modern clades (Sprigg, 1949; Retallack, 2007; Wade, 1972; Sperling and Vinther, 2010) or, in complete contrast considered as a group, an extinct phylum unrelated to animals (Seilacher, 1992; Seilacher et al., 2003). It has recently been suggested that there are multiple, diverse groups within this biota, with

varying potential relationships with modern taxa (Xiao and Laflamme, 2009; Laflamme et al., 2013). Given the current understanding of early animal evolution, it is likely that some taxa of the Ediacara Biota represent extinct lineages that belong along the animal tree, including those with bilaterian characters (Erwin and Davidson, 2002; Erwin, 2009; Tweedt and Erwin, 2015). This study documenting for the first time, highly regulated growth of an Ediacara taxon, suggests that *Dickinsonia* may represent one of these predicted lineages and that similar examinations of other Ediacara taxa are necessary to gain further insight into the evolutionary history of early animals.

CHAPTER 2: YOU CAN GET ANYTHING YOU WANT FROM ALICE'S RESTAURANT BED: EXCEPTIONAL PRESERVATION AND AN UNUSUAL FOSSIL ASSEMBLAGE FROM A NEWLY EXCAVATED BED (EDIACARA MEMBER, NILPENA, SOUTH AUSTRALIA)

Abstract

We present findings from the newly discovered fossiliferous bed, TB-ARB, from the Ediacara Member exposed at the National Heritage Site, Nilpena Station, west of the Flinders Ranges, South Australia. Due to fine grain sands casting organisms on TB-ARB it contains remarkably preserved Ediacaran fossils, some of which are exceedingly rare, with little evidence for taphonomic disturbance. Here we demonstrate that, despite extraordinary preservation, ecological metrics from TB-ARB are characteristic of those found on other Ediacara Member beds and that this fossil assemblage is consistent with the previously recognised heterogeneity of the Ediacaran seafloor. This result suggests that limited taphonomic processes identified on more typical beds at Nilpena do not bias our view of Ediacaran palaeoecology, but together, these beds present a complete picture of ancient animal communities. Remarkable preservation of rare *Andiva ivantsovi* allows investigations of morphology, growth and life habit. We identify complex growth in this organism that maximizes surface area relative to volume and a morphology consistent with previously unsubstantiated claims for mobility. Features of *Andiva* indicate that it was likely related to two other extinct

Ediacaran flat-lying, modular, mobile taxa, *Dickinsonia* and *Yorgia,* suggesting a possible eumetazoan placement for this organism.

Introduction

Evidence of the first communities of complex, macroscopic organisms is found in the soft- bodied fossils of the Ediacara Biota (Narbonne, 2005; Xiao and Laflamme, 2009; Droser and Gehling, 2015; Droser et al., 2017). Excavation of 35 fossiliferous bedding plane surfaces at the National Heritage Site, Nilpena Station, west of the Flinders Ranges, South Australia (Figure 1), provides the rare opportunity to study palaeocommunities with little time averaging: they are preserved as they would have existed on the Ediacaran seafloor (Droser et al., 2019a). These m^2 scale beds contain hundreds of *in situ,* exceptionally preserved fossils allowing for detailed examinations of the biology and ecology of some of Earth's oldest complex, macroscopic organisms. Such research has yielded essential insight into the earliest animal ecosystems and the evolution of animal life on this planet (Gehling et al., 2005; Droser et al., 2006; Droser and Gehling, 2008, 2012; Zhu et al., 2008; Gehling and Droser, 2009; 2013; Tarhan et al., 2010; 2015; 2016; 2017; Sappenfield et al., 2011; Clites et al., 2012; Xiao et al., 2013; Joel et al., 2014; Evans et al., 2015, 2017; Hall et al., 2015; Droser et al., 2017; 2019a; Paterson et al., 2017).

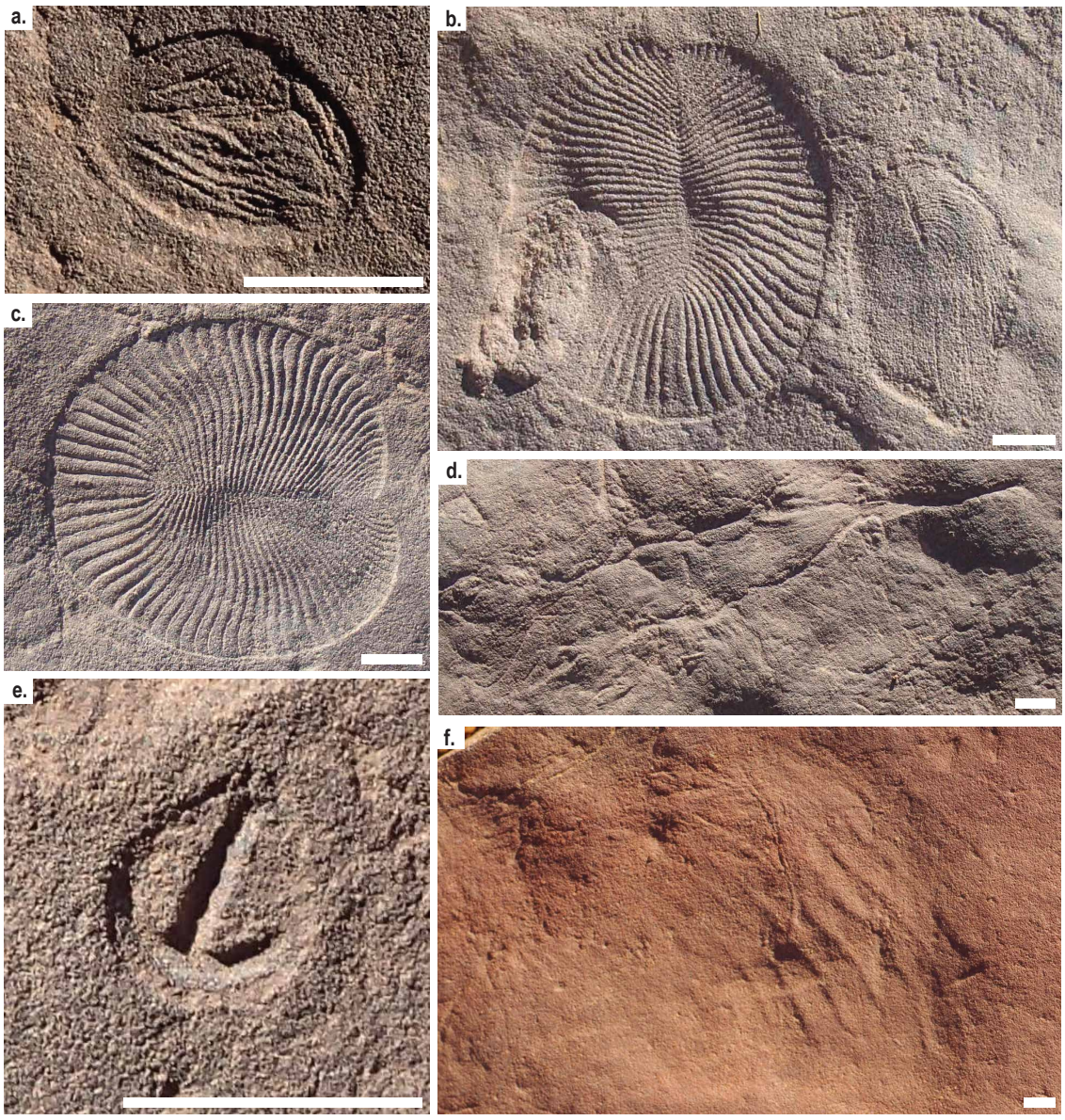

Figure 11. Fossils from TB-ARB, including (a) *Attenborites janeae*, (b, right) *Andiva ivantsovi,* (b, c) *Dickinsonia costata,* (d) bundle of filaments, *Parvancorina* and (f) *Yorgia* “footprint”. All scale bars 1 cm.

In July 2017 a new bed, TB-ARB, was excavated at Nilpena in the same succession as previously excavated beds from the TB site (see Droser et al., 2019a). This bed is atypical in that it contains an unusual fossil assemblage with many otherwise uncommon taxa including *Andiva ivantsovi* Fedonkin, 2002, and, due to finer grain size than usual for Nilpena, all fossils are remarkably well preserved (Figure 11). The abundance of rare taxa and preservation is so striking that the bed was given the ARB designation for Alice's Restaurant Bed, after the Arlo Guthrie song 'Alice's Restaurant Massacree' because, as the song states, "you can get anything you want at Alice's Restaurant."

TB-ARB thus provides an opportunity to evaluate communities of the Ediacara Biota under exceptional preservational conditions and assess the extent to which potential taphonomic bias on coarser grained fossiliferous beds at Nilpena skew our view of Ediacaran palaeoecology and palaeobiology. The abundance of well-preserved *Andiva* allows examination of the growth and life habit of this organism from a single community. Such analysis would not be possible without the numerous specimens preserved in fine-grain sandstone on TB-ARB due to the particularly fine anatomical features and relatively low abundance of *Andiva* in South Australia.

Geologic setting

On the western side of the Flinders Ranges in South Australia, at the Nilpena Ediacara fossil site, the Ediacara Member fills a surface with relief of 10-300 m cut into the underlying Chace Quartzite Member of the Rawnsley Quartzite and occurs 200-600 m below a basal Cambrian disconformity (Gehling, 2000). The Ediacara Member consists of four fossiliferous facies with distinct fossil assemblages preserved in each (Gehling and Droser, 2013; Tarhan et al., 2017). TB-ARB is within the Oscillation-Rippled Sandstone (ORS) facies characterized by thinly bedded, rippled quartz sandstones representing deposition between fair-weather and storm wave-base (Gehling and Droser, 2013; Tarhan et al., 2017). Other fossiliferous beds from the Ediacara Member have been excavated from the poorly sorted Flat-Laminated to Linguoid-Rippled Sandstone (FLLRS) facies characterized by unidirectional flow deposited near wave-base (Gehling and Droser, 2013; Tarhan et al., 2017). Communities of the Ediacara biota are preserved along with the organic mat-bound substrates on which they lived, recorded as textured organic surfaces (TOS), by the deposition of sand during episodic storm surges and flows (Gehling, 2000).

Fossils from the ORS facies occur as casts and moulds on the bases of fine to medium grain sandstone beds. Counterpart casts and moulds of fossils also exist on the tops of underlying beds, but are rarely collectible because these are typically discontinuous and very thin (Droser et al., 2019a; Tarhan et al., 2017).

Sand deposits filled wave ripple troughs after storm events, and were subsequently colonized by microbial mats and benthic macroscopic organisms of the Ediacara biota in the hiatuses between storms. As a consequence, field study is largely confined to the thicker bedded event sands that smothered and moulded the upper surfaces of more resilient organisms, such as *Dickinsonia*, or cast the collapsed bodies of less resilient organisms (Gehling, 1999; Tarhan et al., 2017). The sole surfaces of these event beds are generally cleanly separated from the underlying sands due to early cementation of sand grains via silicification, which lead to the exceptional preservation of the Ediacara Biota (Tarhan et al., 2016).

Materials and methods

As fossils are best preserved on bed bottoms, fossiliferous beds must be systematically flipped and pieced back together to reproduce *in situ* communities, including organic mat-textured surfaces, with ecologically meaningful relationships preserved (Droser et al., 2019a). Such work at Nilpena Station has resulted in the excavation of 30 fossil bearing beds encompassing more than 250 m^2 from the ORS facies. The ORS facies contains iconic taxa of the White Sea assemblage (Waggoner, 2003; Narbonne, 2005) and the highest density and heterogeneity of fossils in the Ediacara Member (Droser and Gehling, 2015; Tarhan et al., 2017). Beds range in total area from 1.1 to 23.4 m^2 with fossil assemblages of variable abundance, ranging from 10-361 individuals, density,

with values of 1-100 individuals per m^2, and diversity, with 1-16 genera per bed (see Table 2 of Droser et al., 2019a).

Once excavated, beds are gridded at the m to cm scale and fossils are mapped with south and east coordinates (see Figure 3 of Droser et al., 2019a). Fossils are documented via latex moulds and digital photography. Measurements are made using digital calipers on latex moulds and from digital photographs using the Image J software, freely available at https://imagej.nih.gov/ij/. Shannon diversity, spatial relations and the Shapiro-Wilk test for normality of *A. ivantsovi* distributions were calculated using PAST (Hammer et al., 2001).

TB-ARB

Newly discovered TB-ARB crops out at the TB site of Droser et al. (2019a) approximately three metres from the original TB excavation pit and less than a metre stratigraphically below TB-BRW. The bed is 8.6 m^2 with an elongated profile (Figure 12a, b). The shape reflects the poor preservation of fossils that occurs where the bed is deeply buried (>1.5 m) and so has not been exposed to sufficient weathering (Droser et al., 2019a). TB-ARB is typically 30-40 mm thick but ranges down to 10 mm in thickness (Figure 12a). It is composed of fine sand.

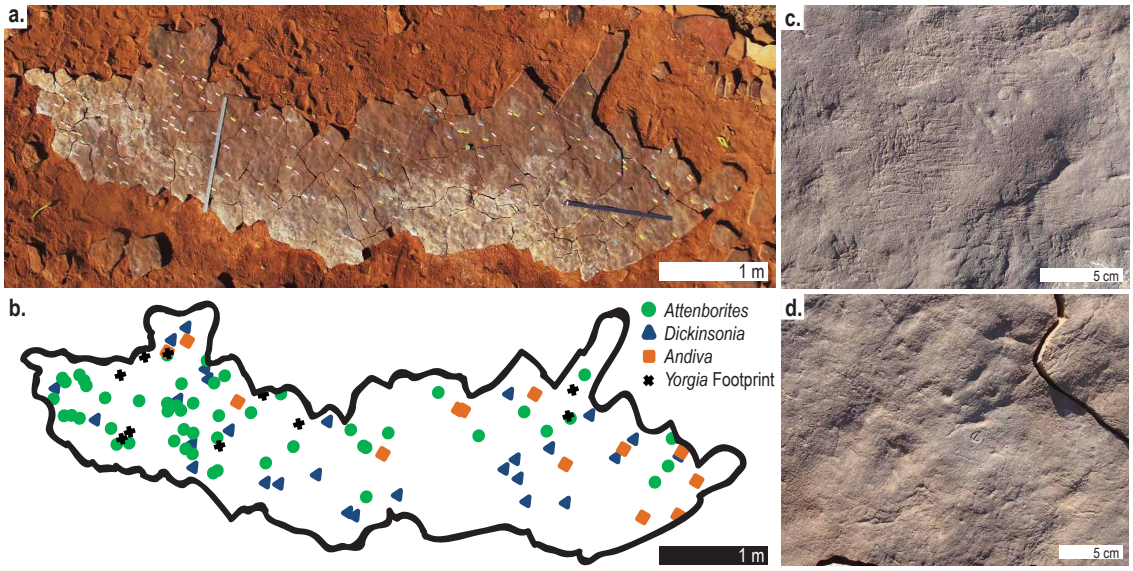

Figure 12. TB-ARB (a) aerial photograph, (b) map with fossils positions marked by symbols and (c, d) complex TOS.

The surface of TB-ARB contains a complex, yet highly organized TOS covering (Figure 12c, d) and abundant, well-preserved fossils. Typically, beds at Nilpena suitable for excavation are recognised by float that can be followed to exposed, outcrop (Droser et al., 2019a). TB-ARB was recognised from float, but significantly less was recovered than expected from such a thick and distinctive bed, and bed outcrop was buried under approximately 50 cm of sediment and displaced sandstone talus fragments.

Preservation

Fossils on TB-ARB are distinctive in that they are exceptionally well-preserved, even for the Ediacara Member (Figure 8). The high fidelity of fossils is likely due

to the smaller grain size of TB-ARB relative to other beds at Nilpena. Specimens of *Attenborites janeae* (see Droser et al. 2019b; Figure 11a), *Dickinsonia costata* (Figure 11b, c), bundle of filaments (Figure 11d) and *Parvancorina* (Figure 11e) are preserved with significant relief (>2 mm, Figure 11a-e) allowing the detailed resolution of minute morphological features (Figure 13). Other fossils exhibit less relief but are still exceptionally well-preserved allowing the identification of sub-mm scale features, such as the modules of *Andiva* (Figure 11b, see below).

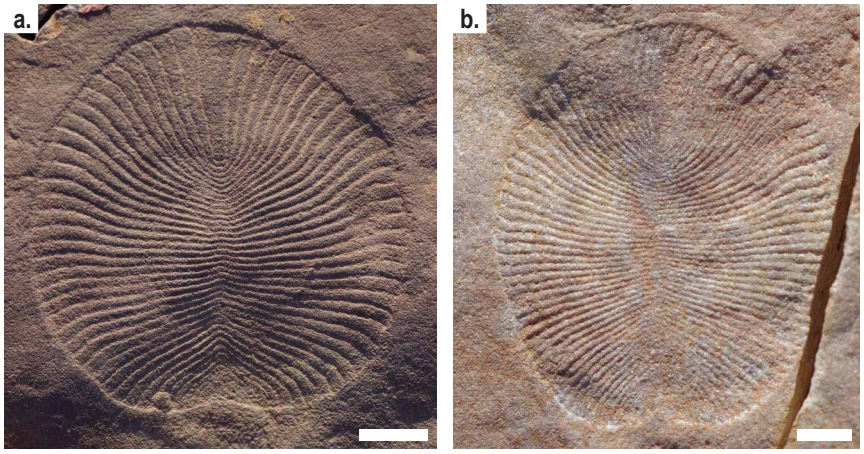

Figure 13. *Dickisnonia costata* from (a) TB-ARB, notice sharp, well-defined outer margin and crisp modules relative to (b) well-preserved specimen from medium-grained STC-B bed. Notice that all features are recognisable in both specimens, but the relief and definition are significantly stronger in the specimen from TB-ARB. (a) TB-ARB 008. (b) STC-B 001. All scale bars: 1 cm.

Fossil assemblage

TB-ARB preserves a fossil assemblage unique to that of any other bed described from the Ediacara Member (Figure 14; Droser and Gehling, 2015; Coutts et al., 2016; Reid et al., 2017; Droser et al., 2019a;). This bed contains taxa typical of the White Sea assemblage, such as abundant *D. costata* and the algae bundle of filaments, as well as less common *Spriggina, Parvancorina,* and *Coronacollina.* The two most common fossils at Nilpena, *Aspidella* and *Funisia*, are either absent or represented by a single specimen, respectively. TB-ARB also contains some particularly rare fossil taxa. The most abundant fossil is the newly named *Attenborites* with 52 specimens, otherwise known from two other occurrences on Nilpena bed 1T-F and 12 specimens from the Ediacara Member elsewhere in the Flinders Ranges area (see Droser et al., 2019b). Unfortunately, statistical analyses of spatial relationships are hampered by the elongated, irregular shape of TB-ARB, however, nearest neighbour analyses indicate that *Attenborites* are distributed randomly.

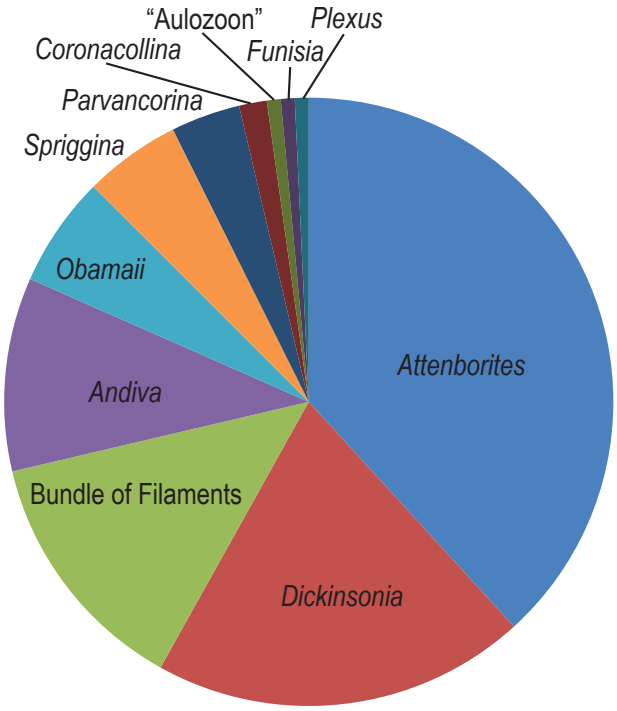

Figure 14 – Pie chart of relative proportions of fossil taxa on TB-ARB. Total number of specimens is 136.

There are 12 specimens of *A. ivantsovi* (Figure 11b) on TB-ARB and four additional specimens were recovered from float. *Andiva ivantsovi* was named based on more than 50 specimens from the White Sea region of Russia (Fedonkin, 2002), but less than 15 have been previously recovered from the Ediacara Member and, on beds at Nilpena, only a single, poorly preserved specimen has been identified within the ORS facies on 1T-F. TB-ARB contains eight specimens of the rare, newly named *Obamus coronatus* (see Dzaugis et al., 2018). Additionally, this bed includes "footprints" of *Dickinsonia* and *Yorgia* (Figure 11f), which are interpreted to represent evidence of mobility (Ivantsov

and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010; Ivantsov, 2011; but see Retallack, 2007; McIlroy et al., 2009). While resting traces of *D. costata* are found on several beds, TB-ARB also includes a single "footprint" of *D. lissa,* known from only one other bedding surface, 1T-F, at Nilpena. *Yorgia* "footprints" are similarly rare, known from only eight occurrences on two beds, TC-MM3 and STC-I.

Bed TB-ARB exhibits a wide range of body sizes for discrete fossil taxa ranging from a specimen of *Attenborites* 4.38 mm to a *D. costata* 99.94 mm in maximum length. This, along with the well-developed, complex TOS, muted ripples, and the relatively diverse fossil assemblage preserved on TB-ARB indicate a mature community and extensive time of exposure prior to burial (Droser et al. 2019). The area and total number of fossils on this bed are slightly above average for the ORS facies, while density is somewhat below average (Table I). The total number of genera and Shannon Diversity of TB-ARB are higher than most beds within the ORS facies, but do not exceed maximum values observed for comparable mature Nilpena communities, such as those preserved on TC-MM3 and 1T-F.

Table 1. Paleoecological metrics of selected excavated beds from Nilpena.

Site-Bed	Area (m^2)	# of Fossils	Denisty ($\#/m^2$)	# of Genera	Shannon Diversity	Sand Grain Size
TB-ARB	8.6	136	15.9	11	1.80	Fine
1T-F	23.4	202	8.6	14	2.14	Med-Fine
MM3	19.7	361	16.7	16	1.43	Medium
ORS Avg.	8.3	113	21.4	6	0.92	

There is no indication of current directionality on TB-ARB in large part because ripples are heavily muted by mat development. *Parvancorina,* which are oriented with respect to current on other beds at Nilpena (Paterson et al., 2016), are randomly oriented on TB-ARB. Anchored erect taxa, *Funisia* and bundle of filaments, which might be expected to fall in a consistent direction are not aligned. Lifted edges of *Dickinsonia* are current oriented features found within the ORS facies (Evans et al., 2015). Three specimens of *D. costata* (Figure 11b) and one *A. ivantsovi* (Figure 15a) are lifted on TB-ARB, however lifted portions are randomly oriented.

Examination of *Andiva ivantsovi*

Morphology

A total of 16 specimens of *A. ivantsovi* from TB-ARB exhibit morphologies similar to described specimens from the White Sea region of Russia (Figure 15; Fedonkin, 2002). Fossils are preserved in negative hyporelief, with a variable,

irregular, ovoid to elliptical shape, separated into serially repeated units and divided by a midline parallel to sub-parallel to the long axis. We refer to serially repeated units as modules for the same reasons outlined by Evans et al. (2017) for *D. costata*. The most distinct feature of all *A. ivantsovi* from TB-ARB is the midline, which is largely negative but divided in the centre by a raised ridge (e.g. Figure 15a). The size and shape of modules and, consequently, overall morphology can exhibit significant variability between opposite sides of the same specimen (e.g. Figure 15b). The anterior region in some specimens is marked by an anterior fringe (Figure 15b, c). The anterior fringe of *A. ivantsovi* is less distinct than any other character (Figure 15a-d), and many specimens on TB-ARB lack any evidence of this feature (Figure 15e, f). When present, the anterior fringe gives the slight appearance of an irregular, ribbed structure previously described for this taxon (Fedonkin, 2002), but the size of specimens and poor preservation of the anterior fringe limits further evaluation. There is no outer fringe at the posterior end and modules do not end at a well-defined outer margin, but instead tapper creating an irregular feather-like morphology (e.g. Figure 15e).

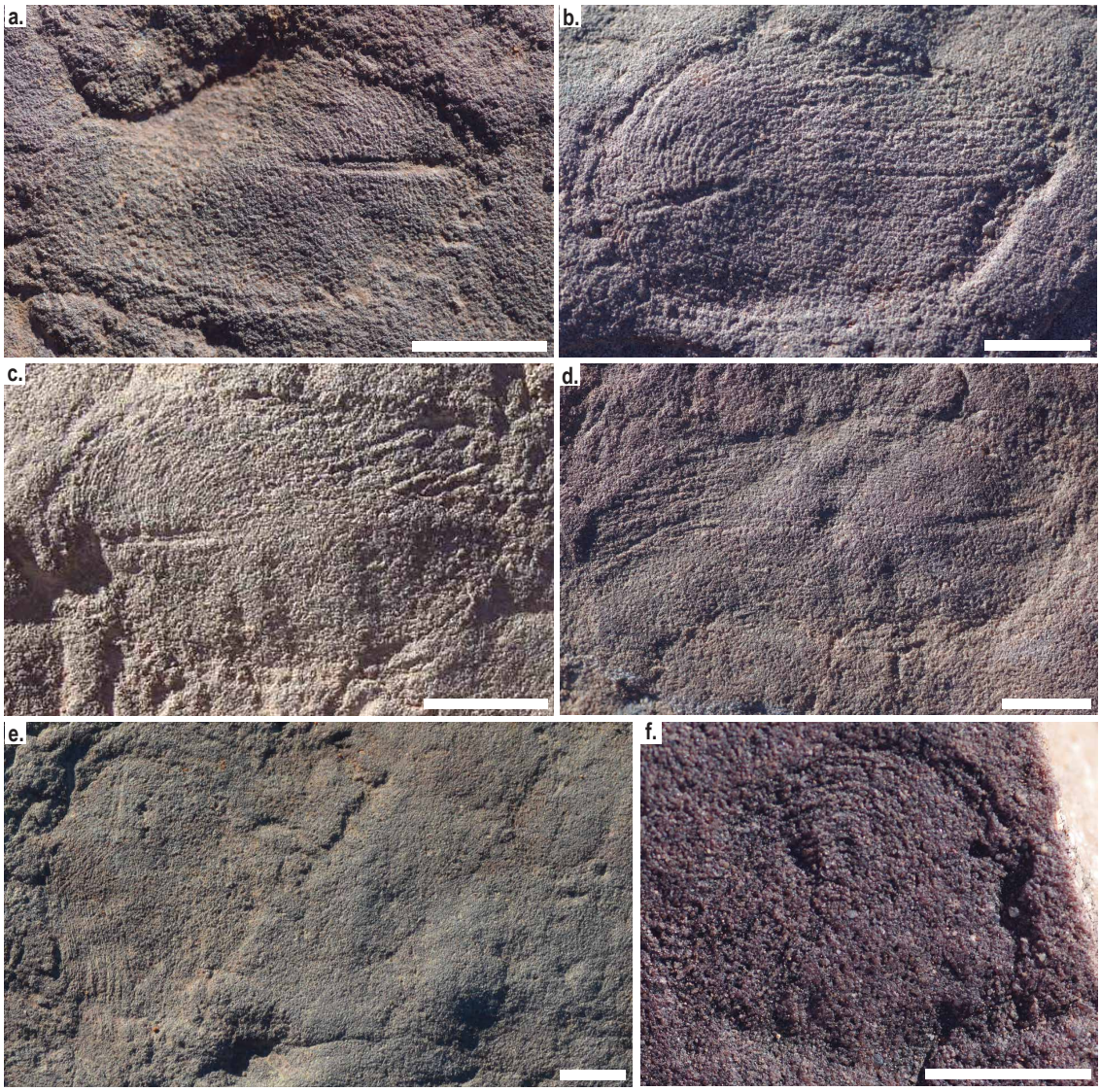

Figure 15 – *Andiva ivantsovi* from TB-ARB. All scale bars 1 cm.

Several features recognised by Fedonkin (2002) are not observed on *A. ivantsovi* from TB-ARB despite the clarity and detail of preservation. We see no evidence of a “post-fringe ridge” creating an anchor-like shape with the midline (Fedonkin, 2002). We also see no evidence of deformation within specimens, which were

attributed to collapse of an originally convex dorsal carapace, or for the presence of “regeneration marks” (Fedonkin, 2002). Fedonkin (2002) also figured specimens of *A. ivantsovi* that exhibited “strong bilateral symmetry”, while a more recently illustrated specimen (Figure 4a-c of Dunn et al., 2017) presents evidence for offset modules. The deep midline preserved in specimens from TB-ARB prevents accurate determination of module symmetry.

Size

Andiva ivantsovi from TB-ARB range in total length from 8.04 to 50.53 mm with an average of 25.96 mm and in total width from 6.99 to 25.08 mm with an average of 17.74 mm. The size frequency distribution is normal (Shapiro-Wilk p-value > 0.05 for unlogged data). Midline length is consistently 45% total length. The relationship between overall length and width is best fit to a power function (r^2 = 0.93, Figure 16a). This relationship is consistent with allometric growth where, as the organism grew larger, length increased at a faster rate than width. Height is not easily resolved from specimens of *A. ivantsovi* however it is always less than 1 mm and does not vary consistently with size. *Andiva ivantsovi* on TB-ARB have between 16 and 44 modules. There is no significant relationship (R^2 < 0.28 for linear, exponential, logarithmic, and power function models) between number of modules and total length (Figure 16b) in the 11 specimens where an accurate module count was attainable.

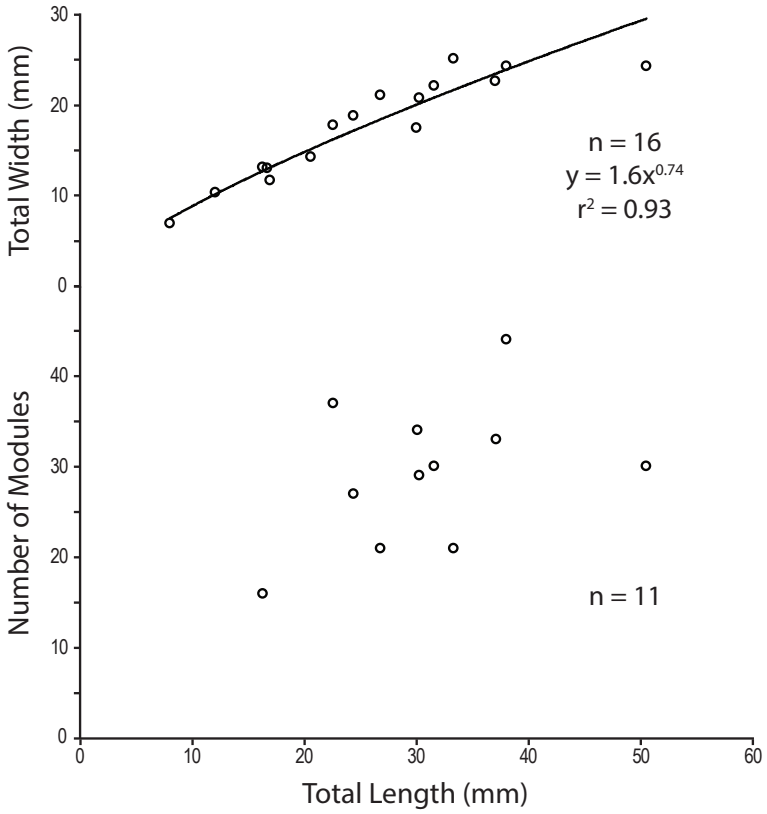

Figure 16 – Size metrics of *Andiva ivantsovi* plotted as total length vs (a) total width and (b) number of modules.

Module width (the distance from the midline to outer margin) was measured in 4 specimens where preservation allowed. Module width increases from anterior to posterior within a specimen, with a minor decrease in size for the five to 10 posterior-most modules (Figure 17). Module length was difficult to resolve even with the superb, fine-grained sand preservation on TB-ARB, however, it appears to be conserved at the midline and, due to geometry, must lengthen at the outer margin, consistent with previously reported growth analysis (Fedonkin 2002).

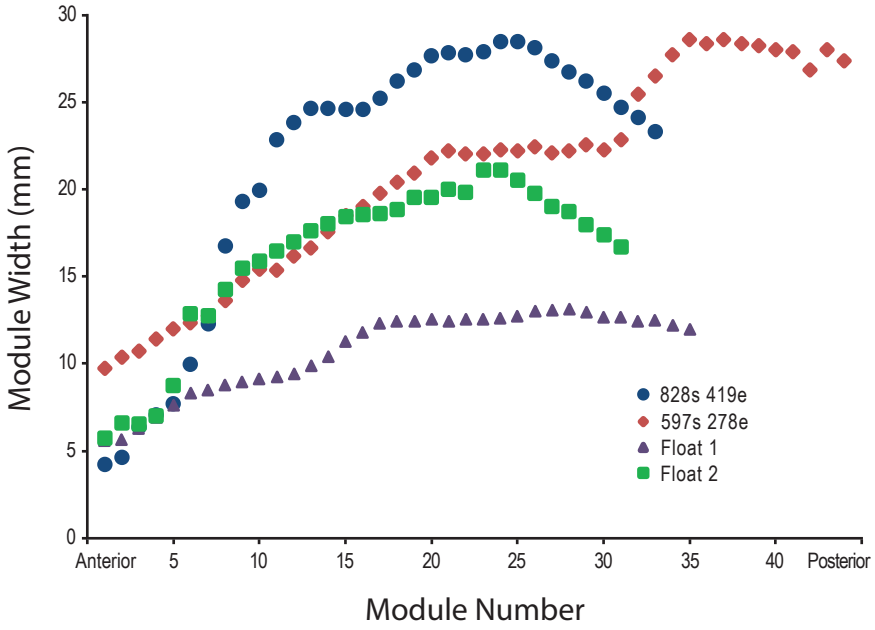

Figure 17 – Graphical representation of changes in module width for *Andiva ivantsovi* from anterior to the posterior, with one representing the anterior most module.

Reconstruction

Specimens of *A. ivantsovi* from TB-ARB support the general morphology outlined by Figure 5 of Fedonkin (2002). The main difference between specimens reported from the White Sea region (although see Figure 4a of Dunn et al., 2017) and those presented here is the lack of deformation recorded in Nilpena specimens despite an irregular and variable morphology. This observation is not consistent with the reconstruction of *Andiva* as a convex, carapace bearing organism (Fedonkin, 2002), especially given that abundant *Attenborites* on TB-ARB display clear evidence of collapse (Figure 11a; see Droser et al. 2019).

While the poor resolution of the anterior fringe in specimens from South Australia suggests that this feature was less resilient than the rest of the body, there is no indication of a hard chitinous carapace. Instead, specimens from TB-ARB support *Andiva* as a flat lying organism similar to *Dickinsonia* and *Yorgia*. We attribute the deformation found in previously illustrated specimens as the folding and wrinkling of a flat, soft-bodied organism, comparable to that previously recognised in specimens of *Dickinsonia* (e.g. Figure 7 of Gehling et al., 2005). A recently illustrated specimen (Figure 4a of Dunn et al., 2017), while clearly lifted and folded at the margins, does not contain wrinkle marks inside the body, further supporting the reconstruction of *Andiva* as a flat-lying organism. "Regeneration marks" inferred by Fedonkin (2002) are more parsimoniously attributed to lifted or folded specimens. This suggests that specimens of *Andiva* from the White Sea region underwent more significant biostratinomic alteration prior to preservation than those on TB-ARB, consistent with the exceptional preservation, fine grain size and lack of current oriented features reported here.

Growth

Total length, width and height relationships of *A. ivantsovi* are similar to those identified for *D. costata* (Evans et al., 2017) suggesting that both organisms grew to maximise surface area. In contrast to *D. costata,* the total length to width ratio in *A. ivantsovi* is indicative of allometric growth and the maintenance of a particular overall shape appears less important (Evans et al., 2017). The number

of modules in *A. ivantsovi* is extremely variable with respect to size, even when compared to *D. costata* (Evans et al., 2017). In general, Figure 16b indicates that this organism likely added modules as it grew. Additionally, three previously illustrated specimens for which length and module were published are both larger and have more modules than any on TB-ARB, further suggesting that *A. ivantsovi* growth was achieved in part by module addition (Fedonkin, 2002; Dunn et al., 2017). However, one of these specimens (Figure 4a of Dunn et al., 2017) is more than 3 times larger than any investigated here and contains only 54 modules. It is unclear what level of variation between specimens from the White Sea and South Australia might be attributed to potential taxonomic differences. Still, this large specimen with few additional modules suggests that growth in *Andiva* occurred in multiple stages, with an initial period of module inflation and addition followed by inflation without module addition. It is also possible, as previously suggested, that there is no relation between module number and size (Dunn et al., 2017), however more data is necessary to assess this hypothesis. Smaller scale variability in module number with respect to total size could either be attributed to the ability of this organism to manipulate shape, a lack of regulation or, more likely, both. The asymmetry about the midline within specimens and feather-like posterior morphology indicates that modules in *A. ivantsovi* were not fixed to a membrane at the outer margin, in contrast to *D. costata* (Evans et al., 2017). This could have significantly hampered the ability of *A. ivantsovi* to regulate module number and shape.

Previous authors have indicated that module inflation in *A. ivantsovi* advanced via constant growth rates (Fedonkin, 2002; Dunn et al., 2017). Measurements of module width for *A. ivantsovi* on TB-ARB demonstrate that, like *D. costata,* modules generally grew wider with age but grew at variable rates depending upon their position within the body (Evans et al., 2017; Hoekzema et al., 2017). Because the widest module in all four specimens analyzed is not at the anterior or posterior-most end, modules must have changed their growth rate at some point. Such developmental patterning demonstrated well-regulated growth to maintain an overall ovoid shape in *D. costata,* and suggests that *A. ivantsovi* utilized gene regulatory networks common to all Metazoa but expressed only in bilaterians today (Erwin, 2009; Evans et al., 2017). The variable shape of *A. ivantsovi* negates regulation of module width exclusively to maintain shape, but growth patterning and similar morphology indicates a level complexity analogous to that of *Dickinsonia.*

The dramatic overall increase in module width from anterior to posterior may indicate module addition (‘differentiation’ of Dunn et al., 2017) at the anterior, immediately behind the anterior fringe. Interestingly, a similar pattern was proposed for *D. costata* based largely on incomplete modules at the anterior end (Hoekzema et al., 2017 but see Evans et al., 2017, Gold et al., 2015; Runnegar, 1982; Sperling and Vinther, 2010). No such incomplete modules were recognised

in *A. ivantsovi* studied here, however one specimen from the White Sea contains evidence of an incompletely inserted module at the posterior (Dunn et al., 2017). Previous analysis of *A. ivantsovi* indicated qualitatively that module length decreases posteriorly (Fedonkin, 2002), which would further suggest posterior addition. Unfortunately, despite the high resolution provided by TB-ARB, measurements of such features would be unreliable. It has been proposed that the youngest modules in a given fossil organism may not always be the smallest (Dunn et al., 2017, Hoekzema et al., 2017) and many characters of Ediacaran taxa can be better explained by taphonomic distortion than evidence of biologically meaningful structures (e.g. Tarhan et al., 2015). Thus, the location of module insertion remains uncertain.

Mobility

Fedonkin (2002) stated that *Andiva* was a "benthic [organism] capable of creeping or gliding across the sea bottom" but provided no evidence for this claim other than similarities with *Dickinsonia* and *Yorgia*, which are interpreted as mobile based on associations with "footprints" (Gehling et al., 2005; Ivantsov and Malakhovskaya, 2002; Ivantsov, 2011). Our analysis of growth and morphology adds to the number of similarities between the three taxa. The recognition that the irregular shape and asymmetry about the midline of *Andiva* is biological rather than taphonomic suggests a surprising amount of flexibility. Given the lack of any evidence for current influence and remarkable preservation of specimens

on TB-ARB, we propose that morphologic variability reflects the ability of this organism to manipulate its body shape independent of growth. A logical explanation for such manipulation is that it is in some way related to mobility. Lifted specimens, similar to those observed in *Dickinsonia,* suggest that *Andiva* was a free-living organism not firmly attached to the Ediacaran seafloor (Evans et al., 2015). Figure 15a shows an asymmetrical specimen, typical of *Anidva,* where the top half appears to be contracted relative to the bottom half. Alternating expansion and contraction of the right and left sides of the body could result in peristaltic movement as is found in basal, non-segmented animals today (e.g. Clark, 1981). The prevalence of the midline in *A. ivantsovi* from TB-ARB suggests that this was likely a resilient feature and if modules where fixed to the midline it would provide the structural support necessary for peristaltic movement (Clark, 1981). Such mobility would most likely require musculature, for which there is little morphologic evidence, however, the complexity and morphological similarity with *Dickinsonia* implies that *Andiva* was at least a eumetazoan grade organism, so the presence of musculature would not be unrealistic. The recognition here that *Andiva* was not concave in life indicates that deformation in specimens from the White Sea, previously attributed to collapse, may instead be the result of muscular contraction.

Interpretations that *Dickinsonia* and *Yorgia* were mobile come largely from associations with “footprints”, most commonly taken to represent areas where

these organisms remained stationary for some period of time, removing the organic mat (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010; Ivantsov, 2011; but see Retallack, 2007; McIlroy et al., 2009). In order to leave the trails of successive "footprints" observed for *Dickinsonia* and *Yorgia* these organisms must have been capable of moving from place to place (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005). No such "footprints" have been identified for *Andiva,* but this does not rule out mobility. "Footprints" are only preserved where mobile organisms had significant impact on the organic mat (Coutts et al., 2016). *Andiva* from South Australia exhibit significantly less relief and are smaller than average for *Dickinsonia* or *Yorgia* (Figure 11b), so this organism would have been less likely to disturb the organic mat surface. It has been proposed that in order to sufficiently perturb the organic substrate to produce "footprints" these structures may be the result of active feeding (Sperling and Vinther, 2010). While this has yet to be definitively documented, *Andiva* could have been mobile without actively feeding on the organic mat surface, and so it would not have left structures suitable for preservation on the Ediacaran seafloor. We propose that similarities with other mobile taxa, variability of shape, free-living life habit, polarity about and integrity of the midline suggests that *Andiva* was capable of mobility via peristalsis.

Implications for Ediacaran palaeoecology

Despite the wealth of information provided by the exceptional material at the Nilpena field site, there is variability in preservation between beds and it is instructive to address the issue of possible biases due to quality of preservation and grain size. When compared with other beds from the ORS facies, TB-ARB is unexceptional in terms of total area, as well as number and density of fossils, indicating that we are not missing significant amounts of data when investigating coarser grained beds at Nilpena. This suggests that previous estimates of the number and density of macroscopic forms on medium to coarse grain sandstone beds is not biased by preservational constraints and is likely representative of the true abundance and density of Ediacaran macroscopic organisms.

The number of genera and Shannon Diversity on bed TB-ARB are elevated relative to the average for the ORS Facies, however, values are comparable with those from other mature fossil communities from Nilpena, such as 1T-F and TC-MM3. This suggests that the timing between depositional events, and thus the amount of time for community development, is a more significant driver of observed taxonomic composition and size distributions than preservation. Obviously, at some level, poor preservation limits the number of recognizable taxa, but within fossiliferous beds at Nilpena such levels are apparently not reached. Diversity indices from TB-ARB similarly suggest that previous assessments of the Ediacaran Biota are not biased by grain size limitations and

accurately reflect the palaeodiversity and evenness of Earth's first macroscopic communities. Further, the assemblage of rare taxa on TB-ARB bolsters previous interpretations of large heterogeneity in the distribution of taxa on the Ediacaran seafloor (e.g. Droser and Gehling, 2015).

Two other fossiliferous bed surfaces, NECP-1 and Crisp Wall, have been described from the Ediacara Member outside of Nilpena (Coutts et al., 2016; Reid et al., 2017). NECP-1 is made up of fine-grained sand from the FLLRS facies, contains large individuals and a complex TOS representing a mature, late-succession community (Coutts et al., 2016). Crisp Wall is composed of medium to coarse sand grains from the ORS facies, contains many smaller individuals and a moderate TOS, indicating an immature community dominated by juveniles (Reid et al., 2017). Both beds are smaller than TB-ARB but contain more, and thus a higher density, of individual fossils, but less total genera and lower Shannon Diversity (Coutts et al., 2016; Reid et al., 2017). All three beds share some classic Ediacaran taxa, including *Coronocollina, Dickinsonia, Dickinsonia* "footprints", and *Parvancorina,* and contain differing assemblages of relatively common and rare fossils (Coutts et al., 2016; Reid et al., 2017). Unlike TB-ARB, both NECP-1 and Crisp Wall preserve evidence of current aligned features, suggesting some minor taphonomic events affected these communities prior to or during burial (Coutts et al., 2016; Reid et al., 2017). Despite ideal

preservational conditions, the newly excavated TB-ARB is representative of previously analyzed bed surfaces from the Ediacara Member.

NECP-1 contains numerous exceptionally small specimens of several taxa, including *Parvancorina* ~1 mm in maximum length (Coutts et al., 2016; Coutts, et al., 2017). The smallest observed discrete body fossils are approximately five times larger on TB-ARB. The recognition of sub-mm features within fossils on TB-ARB (Figures 8, 11) indicates that if smaller specimens where present at the time of burial they would have likely been preserved and identifiable on this bed. This result is consistent with previous observations that some portions of the Ediacaran seafloor were dominated by juveniles, while others contained largely adult populations (Coutts et al., 2016; Reid et al., 2017; Droser et al., 2019a).

While the exquisite preservation of fossils on TB-ARB does not change our overall view of the palaeoecology of the Ediacara Member, it does present a new assemblage of fossils and further strengthens the suggestion that the Ediacara Biota was heterogeneously distributed across the seafloor. Furthermore, TB-ARB allows a more detailed examination of *A. ivantsovi*. The lack of taphonomic deformation on TB-ARB demonstrates that *A. ivantsovi* was a flat lying organism that grew to maximize surface area relative to volume. Module number relative to body size was not well constrained but growth was achieved via module addition and module width increased according to distinctly bimodal rates. Specimens on

TB-ARB contain a suite of characters indicating that *A. ivantsovi* was capable of movement. Similarities between this organism and the complex, bilaterially symmetrical, mobile modular organisms *Dickinsonia* and *Yorgia* suggests that they were related and together represent an extinct lineage of eumetazoans.

CHAPTER 3: SLIME TRAVELERS: EARLY EVIDENCE OF ANIMAL MOBILITY AND FEEDING IN AN ORGANIC MAT WORLD.

Abstract

Mobility represents a key innovation in the evolution of complex animal life. The ability to move allows for the exploration of new food sources, escape from unfavorable environmental conditions, enhanced ability to exchange genetic material and is one of the major reasons for the diversity and success of animal life today. The oldest widely accepted trace fossils of animal mobility are found in Ediacaran aged rocks (635-539 Ma). The earliest definitive evidence for movement associated with exploitation of resources for feeding occurs in the White Sea assemblage of the Ediacara Biota – macroscopic, soft-bodied fossils of Ediacaran age. Here we evaluate potential support for mobility in dickinsoniomorphs, presenting new data regarding abundant *Dickinsonia* and associated trace fossils from the Ediacara Member, South Australia. Results quantitatively demonstrate that *Dickinsonia* was capable of mobility on relatively short, ecological timescales. This organism was bilaterally symmetrical, likely moved via muscular peristalsis and left trace fossils due to active removal of the organic mat related to feeding. Analogous structures associated with *Yorgia* indicate that it was also mobile and fed in a similar manner. Morphological evidence suggests that two other modular taxa, *Andiva* and *Spriggina*, were able to move but did not feed in a manner that impacted the organic mat. Together,

these data suggest that mobility was present in multiple disparate bilaterally symmetrical Ediacaran taxa.

Introduction

Fossils of the Ediacara Biota preserve the oldest macroscopic, community forming organisms on Earth and record a variety of novel animal innovations, including the first evidence of sexual reproduction, scavenging, tiering and skeletonization (Droser and Gehling, 2015; Gehling and Droser, 2018). One particularly significant Ediacaran evolutionary event was the development and diversification of metazoans with the ability to move (Seilacher, 1989; Fedonkin and Waggoner, 1997; Ivantsov and Malakhovskaya, 2002; Jensen, 2003; Gehling et al., 2005). These early mobile animals evolved at a time when the seafloor was covered in a ubiquitous organic mat that was an integral part of the biosphere and an abundant source of potential nutrients for macroscopic Ediacara Biota taxa (Seilacher, 1999; Steiner and Reitner, 2001; Callow and Brasier, 2009; Gehling and Droser, 2009). Importantly, mat bound sand grains created a firm substrate that was difficult to penetrate, but those animals that were capable of generating sufficient energy to disturb such sediment left readily preserved and distinct trace fossils (Seilacher, 1999; Droser et al., 2002).

The Ediacara Biota is classically divided into three temporally sequential assemblages: the oldest Avalon, followed by the White Sea and youngest Nama

(Waggoner, 2003). The earliest evidence of animal movement is reported from the Avalon assemblage (571-557 Ma; Boag et al., 2016) of Newfoundland (Liu, et al., 2010; Menon et al., 2013; Liu et al., 2014; Liu and McIlroy, 2015; although see Buatois and Mángano, 2016; Droser et al., 2017). In contrast, the latest Ediacaran, concurrent with the Nama assemblage (551-539 Ma; Boag et al., 2016; Linnemann et al., 2019), contains multiple, distinct trace fossil genera at numerous localities worldwide (Jensen et al., 2006; Chen et al., 2013; Meyer et al., 2014; Mángano and Buatois, 2014; Buatois et al., 2016; Darroch et al., 2016; Chen et al., 2018). While these structures are commonly attributed to the activity of complex metazoans, research demonstrates that similar trace fossils can be produced by less derived forms, such as protists (Matz et al., 2008) or microbial aggregates under oscillatory flow (Mariotti et al., 2016).

The White Sea assemblage (560-551 Ma; Boag et al., 2016) is known primarily from deposits in Russia and Australia and includes trace fossils representing evidence of mobility by multiple disparate organisms (e.g. Droser et al., 2017). This assemblage records both shallow water, mat dominated ecosystems and diverse Ediacaran organisms capable of mobility (Seilacher, 1999; Gehling et al., 2005; Gehling and Droser, 2009). Crucially, mobile organisms disrupted and exploited organic matter bound in this substrate but not to the exclusion of ubiquitous mat grounds. During the Phanerozoic, efficient bioturbation by metazoans typically leads to an inverse relationship between the presence of

organic mats and animals (e.g. Tarhan et al., 2015). Thus, the White Sea assemblage provides a rare window into complex interactions between abundant metazoans and widespread organic mats at the onset of mat disturbance by animals.

Here we describe evidence of movement in an abundant member of the White sea assemblage, *Dickinsonia,* based on the examination of more than a thousand specimens from the Ediacara Member (Rawnsley Quartzite) of South Australia. We start with a description of the organic mat substrates in which early animal mobility evolved and White Sea taxa that were likely capable of movement. We then present a detailed investigation of the fossil record of *Dickinsonia*, including new data regarding abundant trace fossils. Excavation and reconstruction of Ediacara Member bedding planes at the National Heritage Site, Nilpena provides an opportunity to examine *in situ* relationships between body and trace fossils. Data indicate that *Dickinsonia* was capable of mobility on short ecological timescales, possibly via muscular peristalsis, and likely fed on the organic mat lining the Ediacaran seafloor. Results further suggests that other bilaterally symmetrical taxa with evidence of body manipulation may have been mobile and that a variety of life modes and feeding habits were represented within the Ediacara Biota.

Life in a mat dominated world

Fossils of the Ediacaran Biota record the advent of animal life in shallow marine environments dominated by organic mats (Seilacher, 1989; 1999; Gehling, 1999; Steiner and Reitner, 2001; Bottjer and Clapham, 2006; Callow and Brasier, 2009; Gehling and Droser, 2009; Laflamme et al., 2011). These mats are preserved in the form of textured organic surfaces (TOS), organosedimentary iterative textures indicative of matground development and the interaction between matgrounds, macroorganisms, and mechanical sedimentary processes, abundant in Ediacaran aged deposits (Gehling, 1999; Seilacher, 1999; Dzik, 2003; Callow and Braiser, 2009; Gehling and Droser, 2009; Laflamme et al., 2011; Davies et al., 2016). While these mats likely contained microbial, prokaryotic organisms, the complexity and heterogeneity of such surfaces indicate that Ediacaran mats also contained eukaryotes and large, multicellular organisms (Droser and Gehling, 2015; Droser et al., 2017). Thus, TOS include, but are not limited to, microbially induced sedimentary structures (MISS; Noffke et al., 2001).

TOS can be preserved as discrete, iterated structures such as the classic “old elephant skin” (Figure 18a), analogous to micro-topography found in modern eutrophic ponds, or as dense accumulations of microscopic and macroscopic organisms (Figure 18b; Gehling and Droser, 2009). Such aggregations cover meter to decimeter scale bedding planes without definitive outlines or margins

(Gehling and Droser, 2009; Droser et al., 2019a; Tarhan et al., 2017). Examination of TOS from the Ediacara Member indicates that mat surfaces were remarkably diverse, ubiquitous and heterogeneously distributed across the Ediacaran seafloor (Droser et al., 2006; Droser et al., 2019a; Gehling and Droser, 2009; Tarhan et al., 2017).

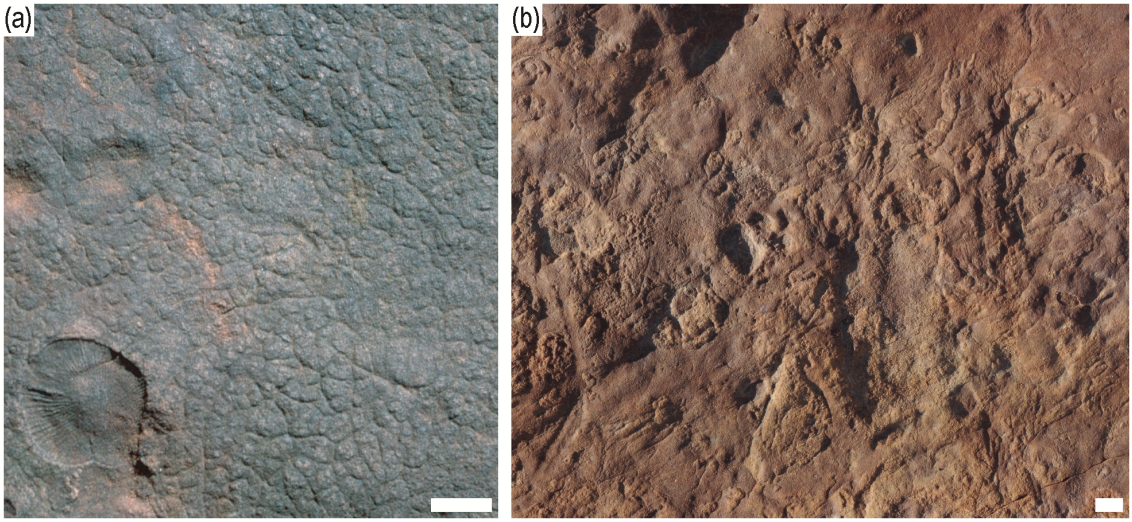

Figure 18. TOS from the Ediacara member, including: a) “old elephant skin” texture, with *Dickinsonia* body fossil in lower left corner, and b) dense aggregation of organic matter from bed TB-BRW. Scale bars 1 cm.

Mats, in some form, were present long before the evolution of animals (Noffke et al., 2001; Noffke et al., 2006; Noffke and Awramik, 2013; Laflamme et al., 2011). During the Ediacaran, mats co-occurred with and were preserved in the same manner as classic, discrete, macroscopic fossil taxa of the Ediacara Biota (Gehling, 1999; Seilacher, 1999; Dzik, 2003; Callow and Brasier, 2009; Gehling

and Droser, 2009). Importantly, such substrates represent a potential source of organic matter for early animals (Gehling et al., 2005; Gehling et al., 2014; Ivantsov, 2009; 2013). Photosynthesis within organic mats may have provided temporary “oxygen oasis” for aerobic organisms (Gingras et al., 2011). Abundant organic matter within mats filled the pore space between sediment that, due to the secretion of extracellular polysaccharides, created a leathery coating, stabilizing the Ediacaran seafloor (Gehling, 1999; Seilacher, 1999). Perhaps most important for paleontologists is the contribution of mats in preserving the Ediacara Biota (Gehling, 1999; Callow and Brasier, 2009; Darroch et al., 2012; Tarhan et al., 2016; Tarhan et al., 2017; Liu et al., 2019).

A major consequence of an Ediacaran seafloor covered in an organic substrate is the preferential preservation of certain trace fossils (Droser et al., 2002). The cohesiveness of Ediacaran mats created a preservational paradox: their ubiquitous presence likely generated the exceptional conditions promoting the preservation of trace fossils, but such structures required specific, energy intensive activity to be produced in relatively firm organic substrates (Seilacher, 1999; Dzik, 2003; Gehling et al., 2005; Buatois and Mangano, 2016). This issue is particularly relevant when considering the early record of animal mobility, where the ability to move evolved in environments characterized by abundant organic mats.

Interactions between mats and macroscopic organisms

While many structures originally interpreted as trace fossils are now recognized as body fossils (e.g. Droser and Gehling, 2008; Sappenfield et al., 2011; Buatois and Mangano, 2016) there are Ediacaran trace fossils that definitively represent interactions between mobile metazoans and mats. *Helminthoidichnites* (Figure 19a) is a cuvilinear trace fossil typically a few millimeters in diameter that occurs in both positive and negative relief on the tops and bottoms of fossiliferous sandstone beds (Jensen, 2003; Droser et al., 2006; Jensen et al., 2006; Gehling and Droser, 2009). The fact that these horizontal burrows are preserved at all indicates the disturbance and likely removal of part of the organic substrate (Jensen, 2003; Droser et al., 2006; Jensen et al., 2006). Commonly preserved levees indicate that the *Helminthoidichnites* progenitor was capable of moving through and displacing sediment (Gehling and Droser, 2009; Droser et al., 2017). This necessitates that the organism that made *Helminthoidichnites* moved in a particular direction, signifying anterior/posterior differentiation, and likely had a hydrostatic skeleton (Budd and Jensen, 2017). These features demonstrate that *Helminthoidichnites,* and similar, contemporaneous trace fossils, represent the earliest definitive evidence for bilaterians in the fossil record (e.g. Jensen et al., 2006; Erwin et al., 2011; Buatois and Mangano, 2016). The recent discovery of *Helminthoidichnites* penetrating body fossils of large discrete taxa suggests that these organisms may have been scavengers, feeding on decayed organic matter from both the mat and buried members of the Ediacara Biota (Gehling and

Droser, 2018). This supports the hypothesis that bilaterians evolved complex behaviors, such as mobility and burrowing, as adaptations for the unique, mat-dominated Ediacaran world (Gingras et al., 2011; Budd and Jensen, 2017).

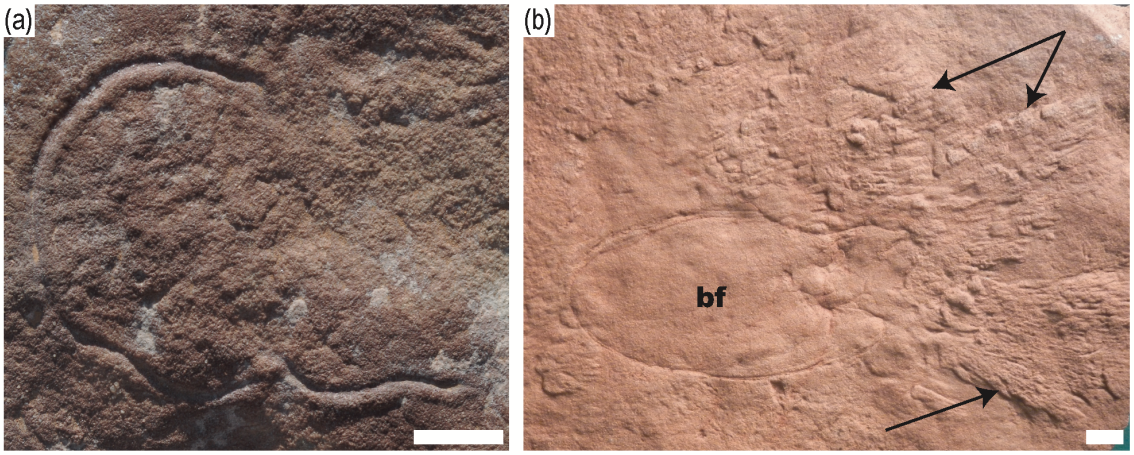

Figure 19. Trace fossils of the Ediacara Biota, including: a) *Helminthoidichnites* and b) *Kimberichnus* (black arrows) with associated *Kimberella* body fossil (bf). (a) TB-S1 001; (b) P35660. Scale bars 1 cm.

Kimberichnus (Figure 19b), paired, shallow ridges preserved in fan-shaped arrays, consistently occur in association with the discrete body fossil *Kimberella* (Fedonkin and Waggoner, 1997; Seilacher, 1999; Gehling et al., 2005; 2014; Ivantsov, 2009; 2013). This suggests that *Kimberichnus* represents scratch marks made by *Kimberella* as it penetrated the cohesive substrate using a proboscis-like structure to excavate and feed on organic matter (Fedonkin and Waggoner, 1997; Seilacher, 1999; Fedonkin, 2003; Ivantsov, 2009; 2013;

Gehling et al., 2014). *Kimberichnus* occur in long repeated sets that far exceed the observed length of the proboscis-like structure used for feeding, indicating that this organism was capable of moving to potential food sources (Ivantsov, 2009; 2013; Gehling et al., 2014). Importantly, like *Helminthoidichnites,* the ability to excavate and disturb sediment suggests the presence of a coelomic cavity, supporting classification of *Kimberella* as at least a stem-group bilaterian (Erwin et al., 2011; Budd and Jensen, 2017).

While associated *Kimberichnus* can be used to infer mobility, no direct traces of movement have been identified from the Ediacara Member (Gehling et al., 2005; 2014), though structures from the White Sea region interpreted as ‘mucus bands’ have been suggested to represent trails of *Kimberella* (Ivantsov, 2009). This highlights that, despite the ability to significantly disturb and remove the organic mat while feeding, whatever method *Kimberella* used to move did not sufficiently displace sediment in a manner conducive to the preservation of trace fossils (Ivantsov, 2013; Gehling et al., 2014). Thus, one of the first, large bilaterians on Earth evolved a feeding strategy adapted to the Ediacaran mat dominated world and without cohesive mat substrates evidence of feeding and mobility would not be preserved.

Dickinsoniomorphs

A third group from the White Sea assemblage, the dickinsoniomorphs, are hypothesized to have been capable of mobility (Fedonkin, 2002; Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005). Dickinsoniomorphs, typified by the namesake *Dickinsonia* (Figure 2, 3) and including *Yorgia* and *Andiva*, are flat, circular to ovoid fossils, divided into iterated units or modules, with anterior/posterior differentiation (Erwin et al., 2011). Dickinsoniomorphs are typically preserved in negative hyporelief on the bases of sandstone beds and occur abundantly in the White Sea region of Russia (Ivantsov, 2007; Zakrevskaya, 2014) and the Flinders Ranges and surrounding regions of South Australia (Gehling and Droser, 2006).

Dickinsonia

With more than 1,300 known specimens, *Dickinsonia* (Figure 3) is the most abundant dickinsoniomorph and one of the most abundant Ediacaran fossil genera from South Australia. There are currently six recognized species of *Dickinsonia: D. costata* Sprigg, 1949; *D. tenuis* Glaessner and Wade, 1966; *D. brachina* Wade, 1972; *D. lissa* Wade, 1972; *D. menneri* Keller and Fedonkin, 1977; and *D. rex* Jenkins, 1992. All but *D. menneri* have been identified from the Ediacara Member. There is some evidence that this number is inflated (Zakrevskaya and Ivantsov, 2017), and that three species – *D. tenuis, D. lissa* and *D. brachina* – may be synonymous (Erik Sperling personal communication,

2019). To avoid confusion and be conservative in our discussion we will refer to all with this general morphology as *D. tenuis*.

Lifted, transported and ripped specimens indicate that *Dickinsonia* was composed of a relatively resilient outer membrane for a soft-bodied organism (Seilacher, 1989; Gehling et al., 2005; Evans et al., 2015). Size frequency distributions from multiple, distinct excavated bedding planes demonstrate that body fossils of *Dickinsonia* are not clustered into similarly sized cohorts, interpreted as evidence for continuous reproduction (Darroch et al., 2013; Evans, 2015; Droser et al., 2019a; Reid et al., 2017; although see Zakrevskaya, 2014). Interpretations of the phylogenetic placement of *Dickinsonia* have varied (Sprigg, 1949; Glaessner and Wade, 1966; Seilacher et al., 2003; Dzik, 2003; Retallack, 2007; Sperling and Vinther, 2010). However, recent biomarker analyses suggests that it was an animal (Bobrovskiy et al., 2018) and a consensus is forming around the hypothesis that *Dickinsonia* exhibits developmental patterns consistent with modern bilaterians (Erwin et al*.,* 2011; Gold et al., 2015; Evans et al., 2017; Hoekzema et al., 2017; Bobrovskiy et al., 2019).

Dickinsonia is an ovoid to elliptical fossil divided longitudinally into modules, ranging in number from 10 to more than 300, with a midline running down the long-axis (Evans et al., 2017, Hoekzema et al., 2017). We follow classic assignments of the anterior as the end with the largest, broadly u-shaped

modules and posterior opposite (Figure 2; Gehling et al., 2005; Sperling and Vinther, 2010; Evans et al., 2017). While the terms “dorsal” and “ventral” have been used in reference to the sediment parallel surfaces of *Dickinsonia*, these terms imply dorso-ventral differentiation and are only applicable to truly bilaterally symmetrical organisms. We refer then to the surface facing up into the water column as the ‘top’ and that remaining in contact with the organic mat as the ‘bottom’ of *Dickinsonia*. Although some controversy exists about the symmetry of modules (e.g. Ivantsov, 2007), specimens from the Ediacara Member consistently demonstrate that the top of *Dickinsonia* was bilaterally symmetrical (Gehling et al., 2005; Gold et al., 2015; Evans et al., 2017). It has been suggested that the bottom of this organism may not have possessed the same symmetry (Wade, 1972; Jenkins, 1992; Budd and Jensen, 2017).

Footprints

The majority of the Ediacara Biota, including dickinsoniomorphs, are preserved in negative hyporelief. Specific taxa, such as the tubular fossil *Funisia*, collapse when buried and produce positive features on the base of beds. However, negative hyporelief impressions of at least two dickinsoniomorphs, *Yorgia* and *Dickinsonia*, are rarely associated with similarly sized positive features of almost identical morphology, referred to as ‘footprints’ or *Epibaion* (Figure 20; Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005). For consistency with previous literature, we follow published terminology and refer to the more common

negative impressions (Figure 3) as body fossils and positive structures (Figure 20) as footprints (Figure 21; Gehling et al., 2005; Sperling and Vinther, 2010; Coutts, Gehling and García-Bellido, 2016). In order to produce positive structures on the base of sandstone beds, footprints would have been depressions in the Ediacaran seafloor subsequently filled with deposited sand during burial.

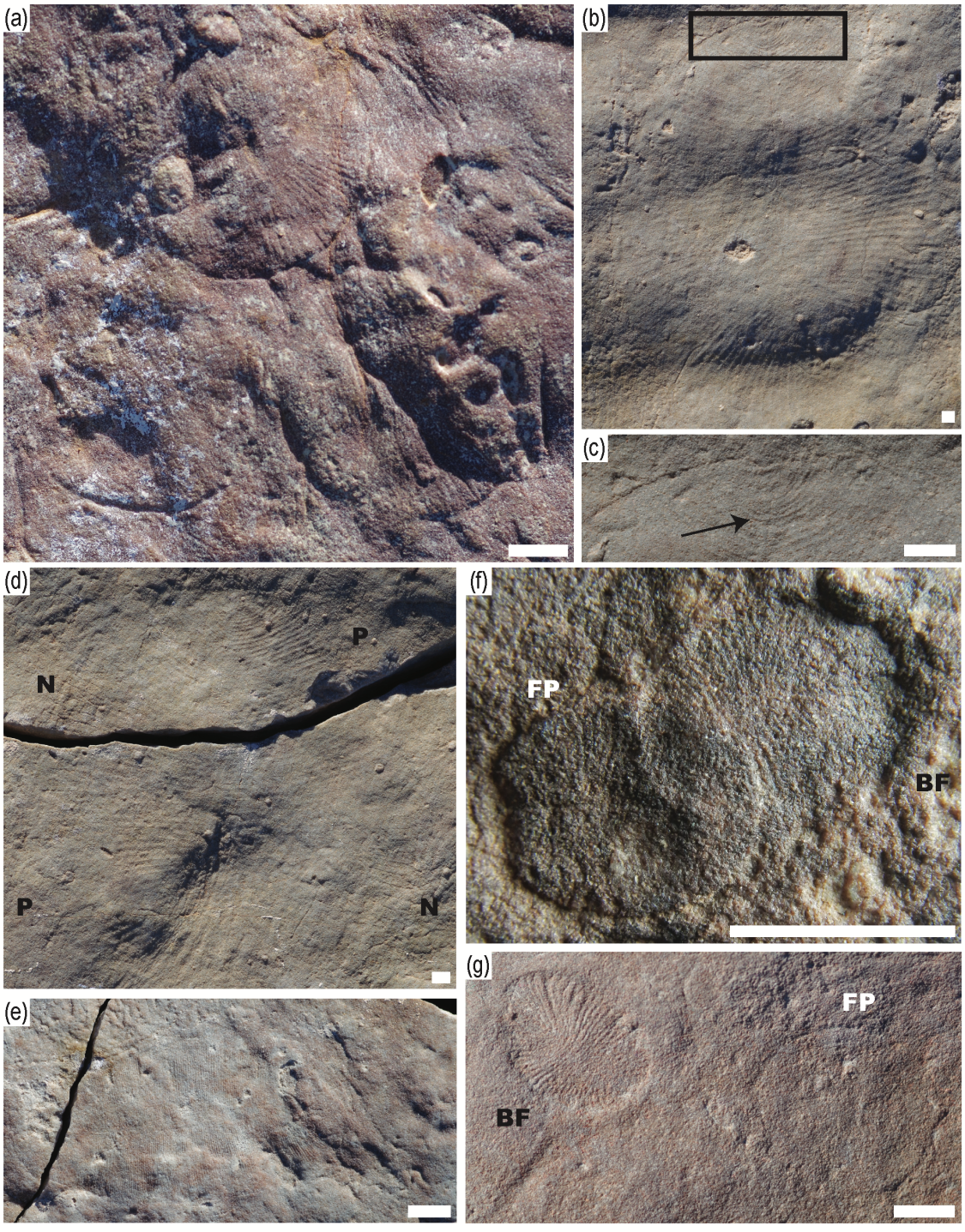
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Figure 20 – *Dickinsonia* footprints, including: a) three associated, similarly sized *D. costata* footprints. b-d) Isolated specimens from 1T-NA (Figure 8), black box in b represents area shown in c. Black arrow in c indicates module symmetry across the midline. Positive (P) and negative (N) module boundaries labelled in d. e) *Dickinsonia tenuis* footprint. f, g) Footprints (f) with associated body fossils (bf). Notice overgrowth of mat in footprints in a-e, as well as atypical, well-defined outer margin of a, b, f and g. a) TB-BRW 001; b, c) 1TNA 001; d) 1TNA 002; e) 1TF 001; f) SAM specimen P40860; g) TC-MM3 001; Scale bars 1 cm.

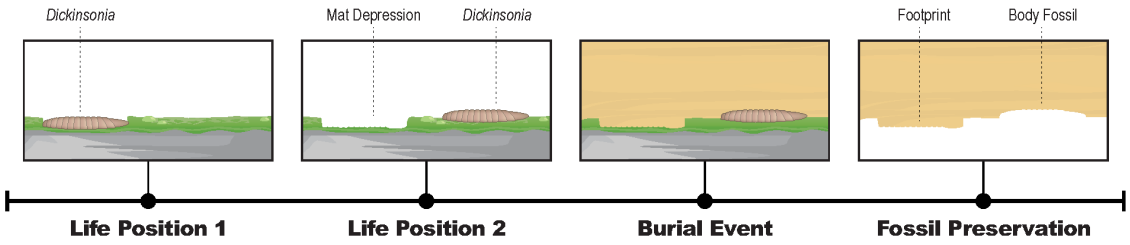

Figure 21 – Timeline of footprint formation and preservation, consisting of: a *Dickinsonia* sitting on and removing the organic mat (life position), followed by the movement of that organism, leaving a depression in the organic mat at its previous location (life position 2), and finally burial of the mat, *Dickinsonia* and depression by sand (burial event) leading to the preservation of a positive footprint and negative body fossil on the base of that overlying sand body (fossil preservation).

Previous interpretations of *Dickinsonia* based on footprints

There are three hypotheses for footprint formation. The most widely accepted is that they are the result of dickinsoniomorphs that remained stationary for a period of time, removed the organic mat beneath them and then moved from that area leaving a depression (Figure 21; Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Fedonkin, 2003; Gehling et al., 2005; Ivantsov, 2007; 2011; 2013; Sperling and Vinther, 2010; Buatois and Mangano, 2016). In this scenario, evidence of mobility between footprints is not preserved because the act of movement did not sufficiently disturb the organic mat (Gehling et al., 2005; Coutts et al., 2016). If

footprints represent active mobility in *Dickinsonia*, we would predict movement to have occurred in a preferred orientation with respect to individual morphology. Under this hypothesis, larger dickinsoniomorphs would likely have been capable of moving greater distances. Movement would have been during life and so would not have been detrimental to *Dickinsonia*. Therefore, we would expect to find a range of preservational variants, including well-preserved footprints and associated body fossils.

Alternatively, it has been proposed that footprints were formed by organisms that died and underwent significant amounts of decay prior to burial (Retallack, 2007). This interpretation is based on the suggestion that dickinsoniomorphs represent terrestrial fungi or lichen, which has largely been debunked (Sperling and Vinther, 2010; Evans et al., 2015; Tarhan et al., 2017; Lücking and Nelson, 2018). Regardless of affinities, the hypothesis that these represent degraded individuals can be tested. For example, if decay produces the change in relief observed between body fossils and footprints, specimens clearly dead long before burial should be preserved in the greatest positive relief. We would also predict footprints to be systematically poorly preserved relative to body fossils.

McIlroy, Brasier and Lang (2009) periodically disturbed a dead thallus of brown algal seaweed sitting on living algal mats resulting in a third hypothesis for footprint formation. This disturbance, followed by resettling of the macroalgae in

a new location, produced depressions in the mat. This suggests that footprints could have been produced when currents transported dickinsoniomorphs (McIlroy et al., 2009). If footprints formed via passive transport, they should exhibit predominantly linear arrangements (Sperling and Vinther, 2010). When preserved on the same bedding plane, they are also expected to be aligned with respect to paleocurrent directionality, as has been observed for other current derived Ediacaran features (Tarhan et al., 2010; Evans et al., 2015; Paterson et al., 2017; Droser et al., 2019a). This is distinct from the preferred orientation predicted in the active mobility hypothesis: mobile organisms move in a preferred direction (i.e. forward) but they do not necessarily move in the same direction as their neighbors or paleocurrent.

Of those authors who agree that footprints represent evidence of active mobility, there is still debate as to what they tell us about dickinsoniomorphs. The method of mobility is unknown, although muscular expansion and contraction (Runnegar, 1982; Gehling et al., 2005) and ciliary crawling (Ivantsov, 2011) have been proposed. It has been suggested that footprints represent evidence of mat removal related to feeding, via either ventral external digestion (Sperling and Vinther, 2010) or ciliary action (Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Ivantsov, 2011; 2013). Coherent ridges in rare trace fossils have been interpreted as evidence of internal digestive processes (Ivantsov, 2011). However, it is possible that simply by remaining stationary for an extensive period

dickinsoniomorphs passively destroyed the organic mat by limiting their access to vital nutrients (Gehling et al., 2005). Below we present new data regarding body fossils and footprints of *Dickinsonia* and *Yorgia* in order to test the three hypotheses for footprint formation and determine what information footprints provide about the biology and ecology of dickinsoniomorphs.

Geologic setting

Fossils of the Ediacara Biota, including abundant *Dickinsonia*, occur within the Ediacara Member of the Rawnsley Quartzite in the Finders Ranges area of South Australia (Figure 1; Gehling and Droser, 2013). The Ediacara Member has not been dated but stratigraphic position and correlation with other units suggest an age range of 560-551 Ma (Gehling, 2000; Boag et al., 2016). This unit is comprised of sandstone beds recording a series of depositional environments, ranging from storm-dominated, shallow marine settings to the slopes and floors of deeper-water incised valleys (Gehling and Droser, 2013; Tarhan et al., 2017; Reid et al., 2019). The Ediacara Member is divided into four fossiliferous facies based on differences in depositional setting, from shallowest to deepest they are the: Flat-Laminated to Linguoid-Rippled Sandstone (FLLRS); Oscillation-Rippled Sandstone (ORS); Planar-Laminated and Rip-Up Sandstone (PLRUS); and Channelized Sandstone and Sand-Breccia (CSSB) Facies (Gehling and Droser, 2013; Tarhan et al., 2017). Classic Ediacara Biota fossils of the White Sea assemblage, including *Dickinsonia,* and TOS are most abundant in the ORS

Facies, characterized by thinly bedded, rippled quartz sandstones deposited between fair-weather and storm wave-base (Gehling and Droser, 2013; Droser et al., 2017).

Fossil assemblages in all but the CSSB Facies are preserved in successions characterized by episodic sedimentation, with seafloor colonization by organic matgrounds and Ediacara macrofauna occurring between depositional events (Gehling, 2000; Tarhan et al., 2017). Benthic communities of the Ediacara Biota are preserved as casts and molds on the bases of sandstone beds ("Flinders Style" of Narbonne, 2005). Identical counterpart casts and molds of fossils also exist on the tops of underlying beds but are rarely preserved because these are generally thinly laminated, discontinuous layers (Gehling, 1999; Tarhan et al., 2017).

Paleocurrent indicators

Within the ORS Facies of the Ediacara Member several current derived features have been identified that allow the determination of relative paleocurrent directionality on excavated bedding planes (Tarhan et al., 2010; Evans et al., 2015; Paterson et al., 2017). Biogenic sedimentary structures referred to as mop were left when holdfasts of frond-like organism, such as *Arborea* or *Charniodiscus*, were dragged through and occasionally pulled out of the organic mat substrate, leaving strongly aligned features on the Ediacaran seafloor

(Tarhan et al., 2010). Aligned body fossils of frondose taxa are also found on bedding planes where relatively high energy events have toppled them in an orientation consistent with current flow (Droser et al., 2019a). Incomplete specimens of *Dickinsonia* reflect the insertion of sand below flat-lying taxa and are oriented based on paleocurrent directionality (Evans et al., 2015; Paterson et al., 2017). *Parvancorina* appears to have been capable of orienting its surface morphology with the prevailing current (Paterson et al., 2017; Darroch et al., 2017; Coutts et al., 2018).

Materials and methods

Ediacara fossils have been recovered from outcrops of the Ediacara Member in the Flinders Ranges and surrounding regions, with extensive collections housed in the South Australia Museum in Adelaide. Importantly, at the National Heritage Nilpena Ediacara fossil site, located west of the Flinders Ranges, thousands of *in situ* Ediacaran fossils have been recovered (Droser and Gehling, 2015; Droser et al., 2019a). Because fossils are best preserved on the base of Ediacara Member beds, systematic excavation and reassembly of bedding plane surfaces is necessary and has resulted in the reconstruction of more than 300 m^2 of *in situ* Ediacaran paleocommunities from the ORS and FLLRS Facies (see Droser et al., 2019a for a detailed discussion). This unique process reveals Ediacaran aged fossils with ecologically meaningful relationships preserved, including complex relationships between organic mats and macrofossils. All specimens

examined as part of this study are either stored and catalogued at the South Australia Museum (identified by SAM P numbers) or remain at the Nilpena field site on excavated bedding planes where their sedimentological context remains intact (labelled by the site and bed on which they are found, e.g. TB-ARB).

Analysis was conducted on 1,353 body fossils and 130 footprints of *Dickinsonia* from the Ediacara Member. We also examined 11 body fossils and 42 footprints of *Yorgia* as well as body fossils of 36 *Andiva* and 74 *Spriggina*. Fossil specimens were documented, and qualitative morphological characters were recorded using digital photographs and/or latex molds. When preserved on excavated, discrete bedding planes, orientation data and relationship to other taxa were mapped and recorded (Droser et al., 2019a). The preferred orientation of current aligned features has been previously reported (Tarhan et al., 2010; Evans et al., 2015; Paterson et al., 2017). Size and distance to relevant structures were measured using digital calipers on fossil specimens and latex molds, or digital photographs and the freely available Image J software (https://imagej.nih.gov/ij/). Orientation data for successive trace fossils were obtained using Image J. We used the Rayleigh's and Rao's spacing tests for uniform distributions to nonparametrically analyze directional data (Davis and Sampson, 1986; Hammer et al., 2001). Both methods assume the null-hypothesis that a given data set is randomly distributed, with the Rayleigh's test assuming unimodally distributed data (Davis and Sampson, 1986; Hammer et al.,

2001). Both have been applied to modern mobile organisms to test for preferred directions of movement (Santos et al., 2010; Aloy et al., 2011). Relevant p-values for these statistics were computed using the PAST software (Hammer et al., 2001).

Results

Of the *Dickinsonia* body fossils identified, 1,160 are *Dickinsonia costata*, 128 are *D. tenuis* and 55 are *D. rex,* compared with "footprints" of 118 *D. costata*, 8 *D. tenuis* and 4 *D. rex.* Body fossils of *Dickinsonia* occur in all fossiliferous facies of the Ediacara Member (Gehling and Droser, 2013) and on 32 of 35 excavated bed surfaces at Nilpena in association with a variety of body and trace fossils as well as variable TOS (Droser et al., 2019a). Footprints have been identified within the FLLRS and ORS facies and they occur on 10 of 35 Nilpena beds (Coutts et al., 2016; Droser et al*.,* 2019a). Bed TC-MM3 preserves the most abundant footprints and body fossils of *Dickinsonia*, and typically there is a positive correlation between body fossil abundance and the presence or absence of footprints*.* Beds 1T-F, TB-ARB and TB-BRW contain well-preserved footprints (Figure 20a) and have been previously interpreted to represent mature communities with little evidence of paleocurrent disturbance (Droser et al., 2019a; Evans et al., 2019a).

Morphology

Dickinsonia body fossils have sharp, well-defined ovate outer margins and module boundaries preserved as thin, negative relief grooves. Body fossils can be incomplete due to the lifting of part of the organism off of the substrate during burial (Evans et al., 2015). Even in these body fossils the outer margin is distinct (e.g. Figure 2 of Evans et al., 2015). Less than 2% of all *Dickinsonia* body fossils are overprinted by TOS or other macroscopic body fossils. *Dickinsonia* body fossils do not overlap, and when close enough to potentially meet they display evidence of avoidance behavior (Figure 10 of Gehling et al., 2005). The midline is not always preserved, even in pristine specimens of *Dickinsonia* (Figure 13), but when present is typically expressed in negative hyporelief (Figure 22a). In life, *Dickinsonia* would have been a relatively flat organism several millimeters in total thickness with module boundaries and midline expressed as faint ridges.

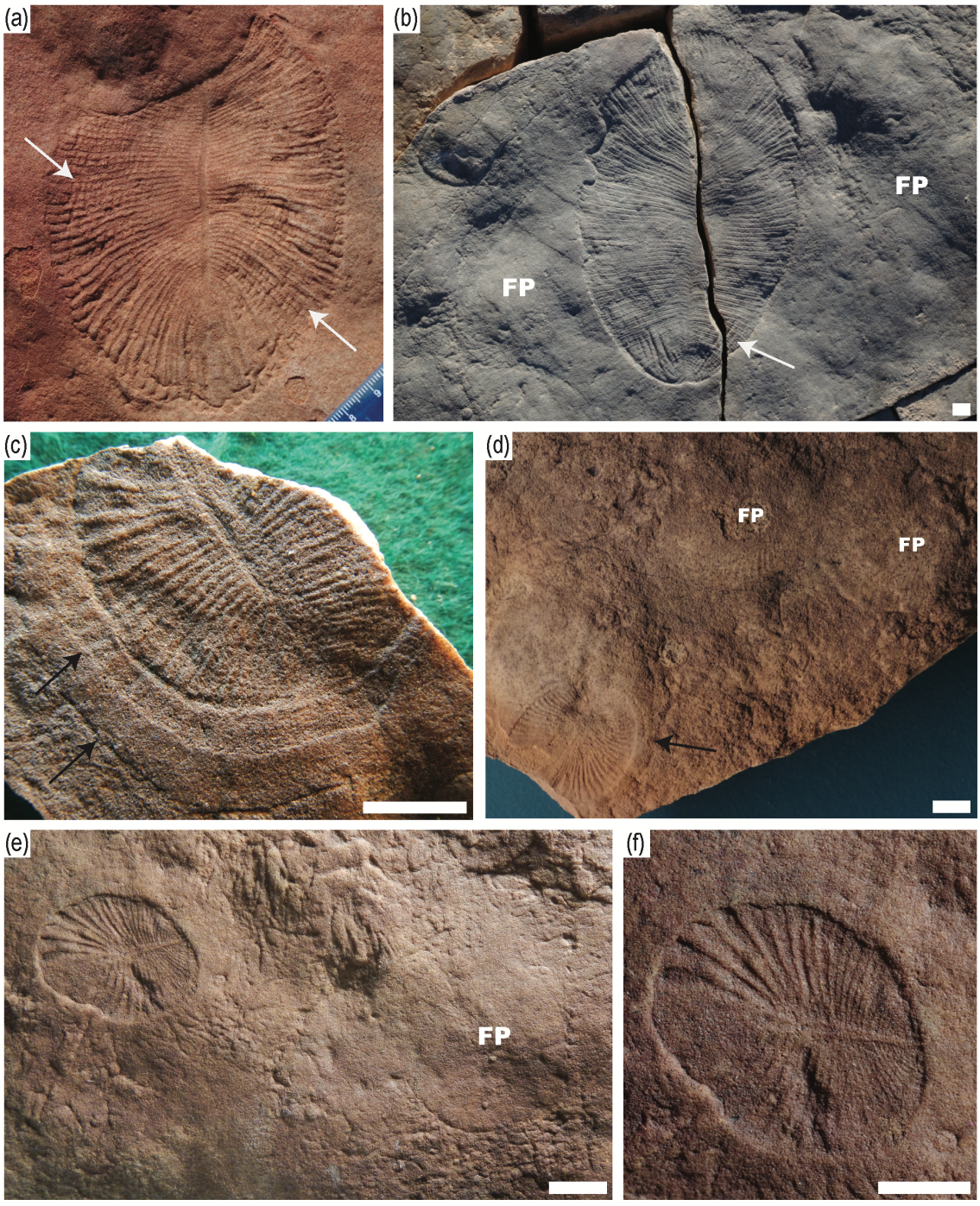
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Figure 22 – Morphological features of *Dickinsonia*, including: a, b) wrinkled specimens, notice that (b) is sitting in its own footprint (FP) and is therefore significantly contracted, arrows indicate wrinkle marks; c, d) contracted specimens, notice (d) is associated with similarly sized footprints, arrows indicate contraction rims; e, f) irregularly shaped *Dickinsonia* associated with a similarly sized footprint (e) and close up of *Dickinsonia* body fossil (f) top anterior expanded relative to the rest of the body. a) 1T Float 001; b) 1TF 002; c) SAM specimen P40944 d) SAM specimen P48729; e, f) SAM specimen P40979. Scale Bars 1 cm.

Of the body fossils investigated here 102 contained wrinkle marks (Figure 22a, b). In all but seven of these specimens, wrinkle marks occur in consistent circular patterns perpendicular to modules, while three specimens exhibit both parallel and perpendicular wrinkles. The location and extent of these structures is highly variable. Within specimens, wrinkle marks do not necessarily follow the same bilateral symmetry exhibited by modules on either side of the midline (e.g. Figure 22a). Many *Dickinsonia* body fossils contain evidence for post burial contraction (Figure 22c, d; Gehling et al., 2005; Coutts et al., 2016; Bobrovskiy et al., 2019). Although specimens exhibit both wrinkling and contraction, these features are found independently. *Dickinsonia* with wrinkling and/or contraction rims on beds such as TC-MM3, 1T-F and TB-ARB are found alongside abundant, well-preserved specimens with no such structures (Droser et al., 2019a; Evans et al., 2019a). Body fossils rarely have an irregular shape with one side of the anterior end of the specimen expanded relative to other portions of the body, which can be associated with footprints (Figure 22e, f).

Data for footprints are presented in Table 2. In general, footprints range from complete, representing the full ovate shape and modular morphology preserved in *Dickinsonia* body fossils, to preserving less than 25% of the total area of the organism. Incomplete footprints commonly exhibit evidence of mat overgrowth or are overprinted by discrete macroscopic fossils, including body fossils and other footprints of *Dickinsonia* (Figure 20a, d, e). The imprint of the middle of the

Dickinsonia is most commonly preserved in footprints. Footprints commonly exhibit poorly-defined outer margins, grading into surrounding TOS. The midline and module boundaries expressed in body fossils are not always preserved in footprints and, when present, occur in variable relief. Modules in footprints meet at the midline and are not offset (e.g. Figure 20c) indicating that the bottom surface of *Dickinsonia* was bilaterally symmetrical.

Table 1. Observed morphologies of footprints from the Ediacara Member.

Footprint character	**Percentage of specimens exhibiting character**	**Number of specimens that exhibit character (of 130)**
Percent of morphology preserved		
- 100%	22	29
- 99-50%	48	62
- 50-1%	30	39
Well-defined outer margin	25	33
Overprinted	91	118
Midline Relief		
- Negative	2	3
- Positive	32	41
- None preserved	66	86
Module Relief		
- Negative	56	73
- Positive	25	33
- Both	12	15
- None preserved	7	9

Size

Body Fossils range in size from a 4 mm *D. costata* (Evans et al., 2017) to a *D. rex* 820 mm in total length (Jenkins, 1992). Footprints range from an 11 mm *D. costata* to a 385 mm *D. rex*, both of which are incomplete, suggesting that the original organisms were significantly larger. On beds at Nilpena, where collection bias is limited (Droser et al., 2019a), the average *D. costata* body fossil is 34 mm in total length with a right-skewed size frequency distribution, whereas the average footprint is 103 mm and has a varied size distribution (Figure 23). The depth of body fossils ranges from less than a mm to as much as 5 mm (Evans et al., 2017). Positive relief of footprints is typically less than that of associated body fossils. Modules in both body fossils and footprints are significantly smaller at the posterior end and get progressively larger in both length and width moving along the body towards the anterior (Evans et al., 2017; Hoekzema et al., 2017).

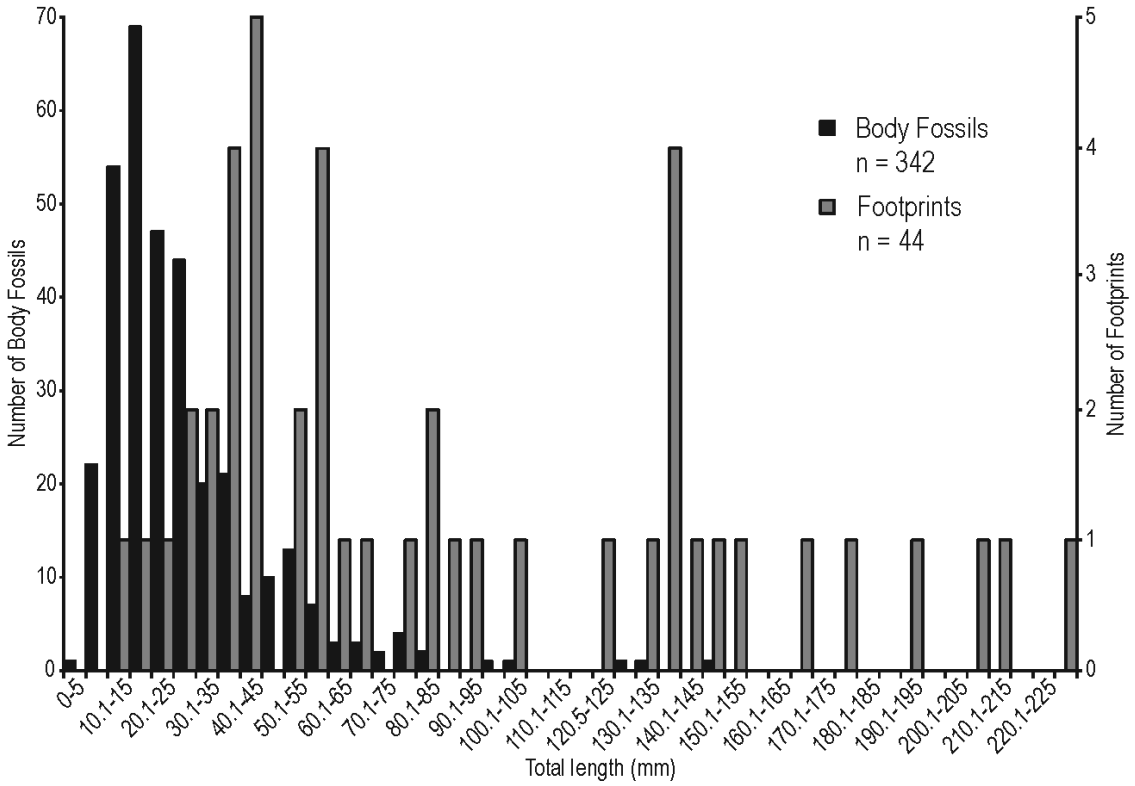

Figure 23. Size frequency distribution of *Dickinsonia costata* body fossils (black bars, left axis); and footprints (grey bars, right axis).

Sets of multiple associated footprints

While they can occur in isolation, similarly sized footprints are observed in close association (Figures 20a-c, 24). Rarely, sets of successive footprints end with a *Dickinsonia* body fossil of similar size and containing the same number of modules. Gehling et al. (2005) indicated that these have a consistent orientation, with the anterior facing the direction of better preservation in associated footprints or towards the body fossil when preserved at the end of a serial set. Of the footprints identified here, 40 are preserved as isolated specimens, 49 are

associated with at least one other similarly sized footprint, 19 are associated with a similarly sized body fossil and 22 occur in association with both. The longest set of footprints consists of 12 positive impressions from bed 1T-NA, which, when complete, are all approximately 140 mm, contain 67 modules, and together span more than 2.5 meters (Figures 20b-d; 24).

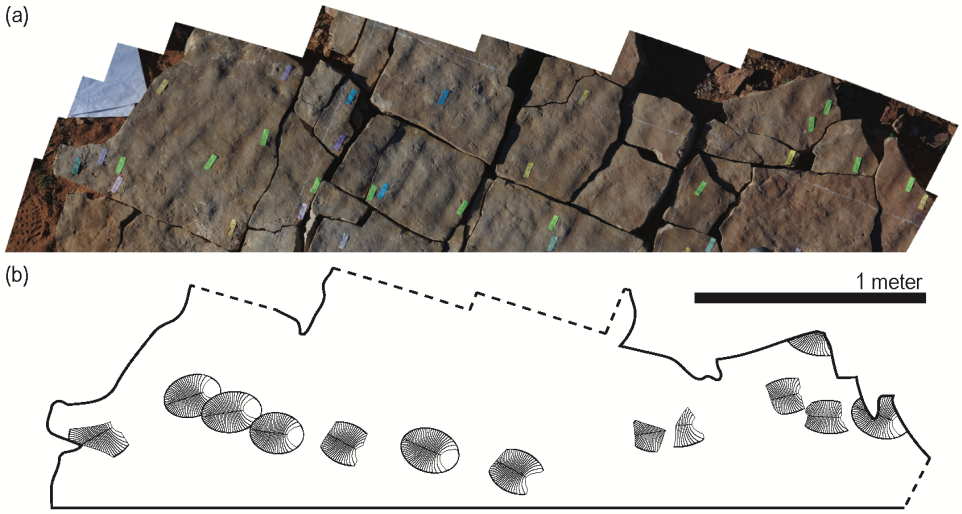

Figure 24. 1T-NA successive *Dickinsonia* footprints: a) bedding plane surface with footprint locations labelled by green post-it notes; and b) line drawing illustrating the position and relative orientation of footprints.

Of the 90 non-isolated footprints 40 show some overlap with associated body fossils or footprints (Figure 20a, b). Overlap is always less than 40% and commonly less than 10% of the total estimated area of the *Dickinsonia.* When associated with body fossils that contain evidence of contraction, footprints are typically the same size as outer contraction rims (Figure 22d). The mean ratio of the distance of displacement – the measured distance between the center of

either two footprints or a footprint and a body fossil – relative to the total estimated length of the *Dickinsonia* that generated them is 1.14, calculated from the 33 footprints interpreted to be at least 90% complete. The greatest displacement is found on bed 1T-F between a footprint and body fossil approximately 15 cm in total length and separated by more than 70 cm.

We have determined the magnitude of displacement and change in orientation of the midline for the 22 specimens, produced by 18 distinct individuals, where these features could be accurately determined (Figure 25). In 11 instances these measurements were made between a footprint and a body fossil. In these examples the formation of the footprint must have preceded the death of the body fossil. When measurements were made between two footprints, we only used overlapping specimens, where one footprint clearly overprints another and can be reliably interpreted as the youngest, or specimens in which the preservation was demonstrably better in one footprint, indicating that it formed closer to the time of burial. In all cases displacement occurred in the anterior direction (positive x-values in Figure 25) and the anterior of the younger specimen faced away from the older specimen. In all but one instance the magnitude of displacement was greater in the anterior direction (positive x-values) than either lateral direction (positive or negative y-values). The change in orientation of the midline varies from 1.3 to 65.4 degrees with an average change of 26.9 degrees. The maximum change in midline orientation is observed

between the footprint and body fossil from 1T-F that exhibit the greatest magnitude of displacement. Both the change in orientation of the anterior and the overall direction of displacement exhibit statistically significant (p-values < 0.001 for both Rayleigh's and Rao's spacing tests for uniformity) deviation from random distributions.

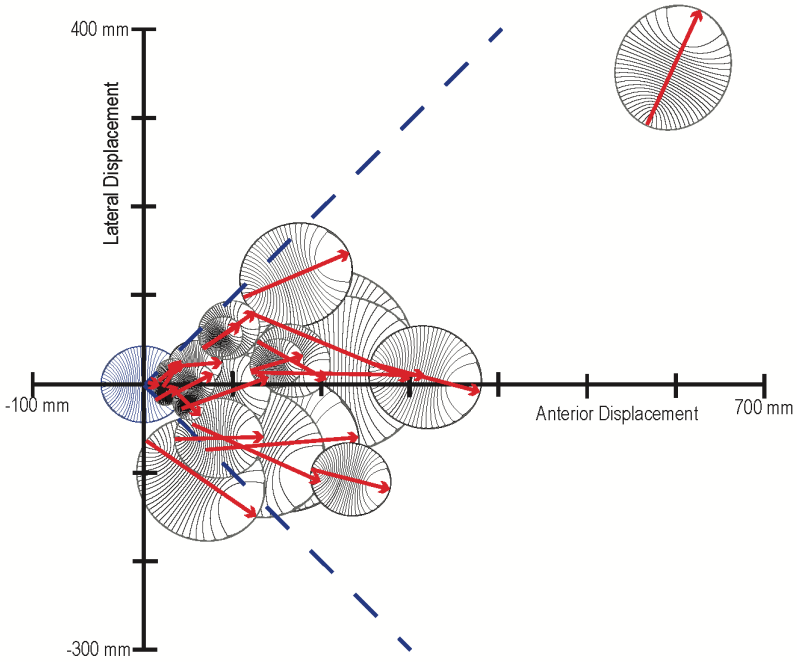

Figure 25. Magnitude of displacement and orientation change observed in *Dickinsonia* body and trace fossils. Blue specimen centered at origin represents the older of the two features normalized so that the anterior of this specimen defines the x-axis. Red arrows demonstrate change in midline orientation. Magnitude of displacement, size of red arrows and specimens are to scale. Dotted blue lines represent 45-degree envelopes (i.e. equal displacement in the x and y directions) thus everything plotted within this envelope exhibits displacement predominantly in the anterior direction.

Comparison with paleocurrent indicators

Bed TC-MM3 contains 206 body fossils of *Dickinsonia* (Evans et al., 2015) and 13 footprints, five of which are preserved in direct association with similarly sized body fossils, allowing a determination of the direction of displacement (Figure 20g). The null-hypothesis of a random distribution for the orientation of the anterior of body fossils (Figure 26a) and of displacement observed between footprints and associated body fossils (Figure 26b) cannot be rejected for either the Rayleigh's or Rao's spacing tests for uniformity (p-values > 0.1). TC-MM3 contains two indicators of paleocurrent directionality, mop and lifted *Dickinsonia,* which demonstrate a coherent current orientation (Figure 26c, d; Tarhan et al., 2010; Evans et al., 2015; Paterson et al., 2017).

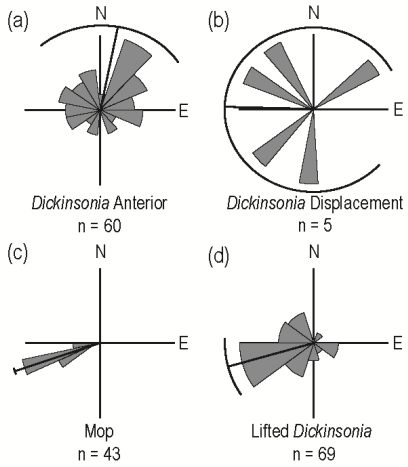

Figure 26. Rose diagrams of features on bed TC-MM3, including the random orientation of: a) the anterior of *Dickinsonia* body fossils; and, b) the orientation of displacement observed in five specimens of *Dickinsonia* body and trace fossils; as well as the current oriented features c) mop; and, d) lifted *Dickinsonia*.

Implications for *Dickinsonia*

Some of the properties of *Dickinsonia* footprints described above – for example the preferential preservation of large footprints and common incompleteness – are consistent with their formation as the result of decay (Retallack, 2007). However, the decay hypothesis is inconsistent with the difference in hyporelief observed between footprints and body fossils. Ripped specimens of *Dickinsonia* (e.g. Figure 9 of Gehling et al., 2005) were clearly dead prior to burial and still leave strong negative impressions, suggesting that *Dickinsonia* was composed of a resilient tissue that did not collapse following death to create depressions in the Ediacaran seafloor.

There is no logical explanation for specimens that were alive at the time of burial (body fossils) to be randomly oriented with respect to one another and exhibit no apparent size selectivity, while those that were dead prior to burial (footprints) occur in a predictable orientation and with others of similar size. Thus, the preferred anterior orientation of displacement and the association of similarly sized footprints are inconsistent with decayed specimens. The recognition of avoidance behavior in body fossils of *Dickinsonia* necessitates that, if they represent decayed specimens, the overlap observed in footprints must be explained by some post death processes, such as transport in paleocurrents. The presence of overlapping footprints on beds such as TB-ARB with little evidence of disturbance (Evans et al., 2019a) is contradictory to the decay

hypothesis. Thus, the origin of footprints as decayed specimens of *Dickinsonia* is irreconcilable with observations of these structures from the Ediacara Member.

The evidence presented here suggests that footprints represent ephemeral impressions of the bottom surface of *Dickinsonia* left in the organic mat. We show for the first time that the direction of displacement of footprints on the same bedding plane, while oriented with respect to the anterior of the *Dickinsonia* that formed them, is random and inconsistent with independent indicators of paleocurrent direction (Figure 26). This alone suggests that they did not form as the result of passive transport (McIlroy et al., 2009). The recognition that body fossils are randomly oriented on TC-MM3 indicates that, if footprints are derived from passive transport, the orientation of displacement should also be random with respect to the morphology of associated body fossils. The consistent anterior displacement observed in successive footprints is incompatible with formation under passive transport. Sets of successive footprints display patterns of displacement ranging from linear to almost completely circular (Figures 20a-c and 22d, e; Figure 1b of Sperling and Vinther, 2010; Ivantsov, 2013; Coutts et al., 2016), contradictory to formation via current transport. Current activity would also be expected to move smaller *Dickinsonia* further distances, inconsistent with our findings (Figure 25).

We find evidence to not only reject the decay and transport hypotheses for footprint formation, but also to accept the proposal that these structures represent areas were *Dickinsonia* remained stationary between periods of active mobility. The consistent anterior direction of displacement suggests an organism whose biology allowed for movement in a particular direction. Well-preserved footprints (Figure 20) are most parsimonious with formation by an actively mobile organism, rather than by some post-death process. The magnitude of displacement, with larger *Dickinsonia* traces typically found further apart (Figure 25), is consistent with active mobility by which larger organisms were capable of moving greater distances.

Footprint timescales and mat regrowth

The recognition that multiple footprints could be produced by the same individual without changes in size or number of modules demonstrates that *Dickinsonia* did not grow between the formation of successive trace fossils. This indicates that mobility occurred on relatively short timescales. We refer to these as ‘ecological’ to represent intervals smaller than those of ontogenetic change, roughly equivalent to timescales of common biotic interactions. Modern microbial mats grow at variable rates, typically on the order of a few mm per year vertically (Sanchez-Cabeza et al., 1999; Buffan-Dubau et al., 2001). Thus, footprints, commonly < 0.5 mm in total relief, would have been obscured by mat regrowth

over much shorter intervals. This suggests that *Dickinsonia* mobility occurred on relatively short timescales, potentially on the order of days to hours.

Distances between footprints demonstrate that *Dickinsonia* could move centimeters to several decimeters at a time, and that over their lifespan moved considerably greater distances. The identification of comparably small footprints suggests that *Dickinsonia* was capable of mobility throughout development. The preferential preservation of large footprints (Figure 23) can be attributed to the longer periods of time required to be obscured by mat regrowth. This, along with the common incomplete nature of footprints, indicates that regrowth of the organic substrate occurred immediately following the movement of *Dickinsonia* from that location.

Dickinsonia **morphology**

Footprints provide the only means for reliably examining the morphology of the bottom surface of *Dickinsonia.* Exquisitely preserved footprints indicate that modules were continuous across the midline on both the top and bottom of specimens from the Ediacara Member (Figure 20c). While module boundaries on the top of *Dickinsonia* were clearly ridges in life, the variability in module relief in footprints prevents a reliable reconstruction of module boundaries on the bottom surface. It is unclear why module relief is inconsistent in footprints, although variable mat composition and regeneration is a probable contributing factor.

Gehling et al., (2005) attributed variable relief in footprints to expansion and contraction of modules. We have since identified specimens with both positive and negative modules on opposite sides of the midline with no difference in module size (Figure 20D), indicating that this discrepancy is not solely the result of variable expansion and contraction. Positive relief module boundaries in footprints would indicate a ribbed morphology on the bottom of *Dickinsonia* identical to that of the top. This prevents the distinction between biradial (no dorso-ventral differentiation) or bilateral symmetry (with dorso-ventral differentiation), however functional disparities may have distinguished the two surfaces (see below).

Anterior-posterior differentiation

Recent debate about the location of module addition has led some to argue that the traditional assignment of anterior and posterior be reversed in *Dickinsonia* (Hoekzema et al., 2017; Dunn et al., 2018). As with body fossils (Evans et al., 2017) we find no evidence in footprints of biologically meaningful (i.e. non taphonomic) incomplete modules at any region of the body – although such evidence would have to be carefully inspected given the irregularity of preservation in footprints – shedding little light on where these structures might have been added. In general, modular organisms, including animals, have various growth patterns (see Gold et al., 2015 and references therein), therefore, we suggest that anterior-posterior designation can be more reliably assigned

based on the preferred orientation of movement. The determination of a consistent direction of movement in *Dickinsonia* supports the classic interpretation of the anterior end as the region with the largest, u-shaped modules.

Comparison with *Phyllozoon*

It has been suggested that *Phyllozoon* (Figure 27) from the Ediacara Member represent trace fossils analogous to *Dickinsonia* footprints (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2007; 2011; 2013). This comparison was based on shared positive hyporelief, division of the body into repeated units, and the lack of well-defined boundaries in both footprints and *Phyllozoon* (Ivantsov, 2013). The morphology of *Phyllozoon* instead suggests that it represents the body fossil of an enigmatic organism (Jenkins and Gehling, 1978). Regardless of affinities, there are several distinctions that separate *Phyllozoon* from footprints. All dickinsoniomorphs are generally ovoid to elliptical in shape, and, though some (e.g. *D. tenuis*) are more elongate, this morphology is inconsistent with the uniform width and tubular shape of *Phyllozoon*. The medial ridge and unit divisions in this taxon are strongly negative, unlike the poorly defined, variable relief midline and modules found in footprints. Unit boundaries in *Phyllozoon* emanate from the medial ridge at a constant angle, maintain a consistent size from the midline to outer margin and are offset (Jenkins and Gehling, 1978). *Dickinsonia* footprints, identical to body fossils of the taxa that made them, meet

the midline at variable angles, can range in size over an order of magnitude within a single specimen and are bilaterally symmetrical (Evans et al., 2017). Modules in *Dickinsonia* and other dickinsoniomorphs exhibit straight to curved, u- to v-shaped morphologies, which, coupled with predictable variations in size, can be used to distinguish between anterior and posterior (Sprigg, 1949; Runnegar, 1982; Gehling et al., 2005; Gold et al., 2015; Evans et al., 2017). *Phyllozoon* module boundaries are linear and it is difficult to identify any anterior/posterior differentiation (Jenkins and Gehling, 1978). When footprints overlap, modules are rarely visible in both specimens, creating cross-hatch type patterns consistent with superimposed and interfered impressions left in the organic mat. In intersecting *Phyllozoon* one specimen clearly overprints the other (Figure 27B). No potential trace maker of *Phyllozoon*, a negative hyporelief structure of similar size and morphology, has been identified within the Ediacara Member. This data suggests that *Phyllozoon* does not represent a trace fossil similar to footprints of *Dickinsonia* and is instead the body fossil of a thin, tubular organism.

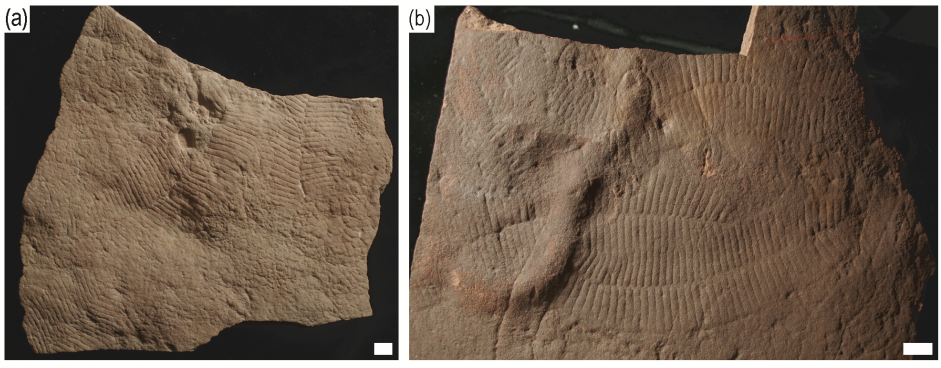

Figure 27. *Phyllozoon* from the Ediacara Member. (a) P49403; (b) P35690. Scale bars 1 cm.

Means of movement

While it is clear that footprints represent evidence that *Dickinsonia* was mobile, discernible trace fossils of active movement are not preserved. This is likely due to the fact that *Dickinsonia* mobility did not disturb the organic mat (Gehling et al., 2005). Runnegar (1982) suggested that wrinkled specimens of *Dickinsonia* are preserved in greater relief than comparable “smooth” specimens, suggesting a maintenance of volume indicative of muscular contraction. The consistent pattern of wrinkle marks in body fossils of *Dickinsonia* perpendicular to modules could have been generated by the contraction of primary muscle bands running parallel to modules (Gehling et al., 2005). The recognition that, when preserved together, contraction rims around body fossils of *Dickinsonia* and associated footprints are similar in size suggests that some amount of contraction could have been the result of post-burial dehydration (Gehling et al., 2005). This may be independent of muscular activity*,* however, the two are not mutually exclusive. Critically, rare wrinkled specimens preserved on the same beds as abundant, well-preserved specimens, which would have undergone identical burial conditions, supports a biological (musculature) rather than taphonomic (dehydration) origin for contraction marks.

While we do not wish to imply a polychaete affinity for *Dickinsonia,* many polychaetes move peristaltically, although commonly aided by cilia and other muscle bands, via alternating expansion and contraction of longitudinal and

circular muscles, with distinct right and left units separated by a midline (Clark, 1981; Purschke and Müller, 2006; Lehmacher et al., 2014). Rare wrinkle marks parallel to modules in *Dickinsonia* may indicate the presence of secondary, antagonistic muscle bands perpendicular to modules. Despite displacement in the anterior direction, small variability in midline orientation and some extent of lateral displacement (Figure 25) suggest that *Dickinsonia* did not move directly forward, consistent with movement via alternating expansion and contraction on either side of a fixed midline. Irregular specimens with one side apparently expanded relative the other and associated with footprints (Figure 22E, F) further support active body manipulation and mobility via alternating muscular activity focused about a fixed midline.

In reconstructing *Dickinsonia* with at least two competing muscle groups, the midline represents a fixed structure upon which muscular expansion and contraction could act. This is supported by the consistent length of modules at the midline (Evans et al., 2017). The lack of a preserved midline in certain specimens of *Dickinsonia* could suggest that this was a fluid filled structure that sometime collapsed or deflated during burial, analogous to a hydrostatic skeleton.

Other possible modes of mobility for *Dickinsonia* include ciliary action and/or active swimming (Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Ivantsov,

2011). We cannot rule out either mechanism as they are unlikely to produce trace fossil evidence on the mat dominated Ediacaran seafloor. Many modern annelids utilize the same muscle configurations adapted for peristalsis in order to move up into the water column (Clark, 1981; Lehmacher et al., 2014) so it is difficult to eliminate potential swimming behavior in *Dickinsonia*. However, it is unclear if this is a viable mode of motility for mature *Dickinsonia,* which can reach more than 80 cm in total length, while maintaining negligible thickness. The close association of successive footprints, typically just greater than one body length apart, may indicate that the energetic demands of swimming were unnecessary to move such short distances.

Mechanism of mat removal

The data presented here allow a reassessment of whether footprints formed as the result of *Dickinsonia* remaining stationary for a sufficiently prolonged period to limit nutrients reaching the mat, possibly including sunlight for photosynthesis (Dzik, 2003), inadvertently destroying it; or, by active removal related to feeding (Gehling et al., 2005; Sperling and Vinther, 2010). A lack of significant overlap between body fossils of *Dickinsonia* has been cited as evidence for digestion through the bottom surface (Gehling et al., 2005). The 1.14 average ratio of displacement to total length likely represents an optimization strategy in which *Dickinsonia* moved enough to gain access to new resources (i.e. organic matter in the mat) while expending as little energy as possible.

The discovery of 12 footprints left by a single individual suggests that many of these ephemeral structures could be formed within a relatively short period. This significantly limits the amount of time for destruction of the mat via passive nutrient limitation at each discrete location and is consistent with more rapid degradation through active feeding. While passive degradation may be expected to leave an impression in the organic mat reproducing the outline of a particular organism, the detailed replication of the bottom morphology of *Dickinsonia* exhibited in footprints is unlikely in this scenario. Active removal of the substrate related to feeding could produce imprints that accurately reflect the bottom surface of *Dickinsonia*, including modules and the midline, especially if such behavior occurred preferentially in different parts of the organism (i.e. at module boundaries).

There is little to indicate how *Dickinsonia* fed. Similar to previous reports from the White Sea region (Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Ivantsov, 2011; 2013) no evidence of ciliary scratching was identified here. The absence of any evidence for a mouth and the fact that footprints sometimes replicated the entire bottom surface of *Dickinsonia* supports some type of ventral digestion (Gehling et al., 2005; Sperling and Vinther, 2010). Whether this was achieved via osmotrophy, chemical release promoting external digestion or a symbiotic relationship with a microorganism capable of degrading the mat remains

unresolved. Gehling et al., (2005) and Ivantsov (2011) identified small bosses between module boundaries in the largest *Dickinsonia* ever discovered and suggested that they may have been related to feeding. Unfortunately, no additional specimens, body or trace fossils, have been identified and their utility remains unknown. We did not find evidence for coherent ridges reported in footprints from the White Sea region (Ivantsov, 2011). While we cannot reject the hypothesis of internal digestion in *Dickinsonia*, some of these structures appear to represent overlapping trace fossils (e.g. Plate 1, Figure 5 of Ivantsov, 2011). Further, variability of module relief in footprints may be the result of irregular mat composition or feeding behavior and is not necessarily indicative of internal digestion.

The recognition of feeding through the bottom surface of *Dickinsonia* suggests that this organism had some level of dorso-ventral differentiation, with the bottom adapted for feeding and the top likely for some other function, possibly gas exchange. These differences would have existed at the cellular level and it is doubtful that they would be recognizable in casts and molds preserved in medium- to fine-grained sandstones.

Phylogenetic interpretation

Analysis of body fossils and footprints of *Dickinsonia* demonstrates that this organism was capable of movement, likely via muscular peristalsis, bilaterally

symmetrical and fed on the organic mat covering the Ediacaran seafloor. Mobility and external ventral digestion were cited by Sperling and Vinther (2010) as evidence that *Dickinsonia* was related to placozoans. Similar to previously described growth patterns (Evans et al., 2017), muscles and bilateral symmetry are not found in modern placozoans (Finnerty, 2005; Botting et al., 2014; Steinmetz et al., 2012). Placozoans change dramatically in size and shape as they move (Pearse, 1989) inconsistent with observations from *Dickinsonia* footprints. This does not rule out the possibility that over the last 550 million years placozoans have undergone significant character loss, but it is also possible that the two simply share a unique ecology.

Most of the characters identified in *Dickinsonia* are common in bilaterians today, especially true bilateral symmetry with dorso-ventral differentiation. However, the presence of muscles and ability to move are not uniquely bilaterian traits and shared gene regulatory networks indicate that more basal animals had the capacity to produce many characters associated with bilaterians today (e.g. Erwin and Davidson, 2002). While the exact method of feeding is difficult to illustrate, the fact that *Dickinsonia* seems to have actively degraded the organic mat over its entire bottom surface is inconstant with a crown-group bilaterian placement, as these organisms almost exclusively feed via an oral opening (mouth). Recent analysis of lipid biomarkers in organically preserved *Dickinsonia* from Russia suggests that it produced cholesteroids, indicative of a metazoan

affinity (Bobrovskiy et al., 2018). Our data further support placement of *Dickinsonia* within an extinct eumetazoan clade that utilized gene regulatory networks common to all animals to produce complex, bilaterian grade body organization (Erwin and Davidson, 2002; Erwin, 2009; Tweedt and Erwin, 2015; Evans et al., 2017; Bobrovskiy et al., 2019).

Other potentially mobile Ediacaran taxa

Footprints and body fossils of *Yorgia* are far less common than those of *Dickinsonia* in the Ediacara Member. However, rare examples exhibit similar features, including overall positive hyporelief, consistent size and anterior displacement, variable module relief, incomplete preservation and the presence of numerous footprints of the same individual as it moved relatively long distances (Figure 28a; Ivantsov and Malakhovskaya, 2002; Dzik, 2003; Gehling et al., 2005; Ivantsov, 2007; 2011; 2013). Body fossils of *Yorgia* are wrinkled in a manner similar to that observed in *Dickinsonia*. Interestingly, the modules of *Yorgia* from the Ediacara member commonly exhibit module boundaries with a regular, crooked or zig-zag pattern (Figure 28b, c). One possible explanation for this is the contraction of muscle bands perpendicular to modules.

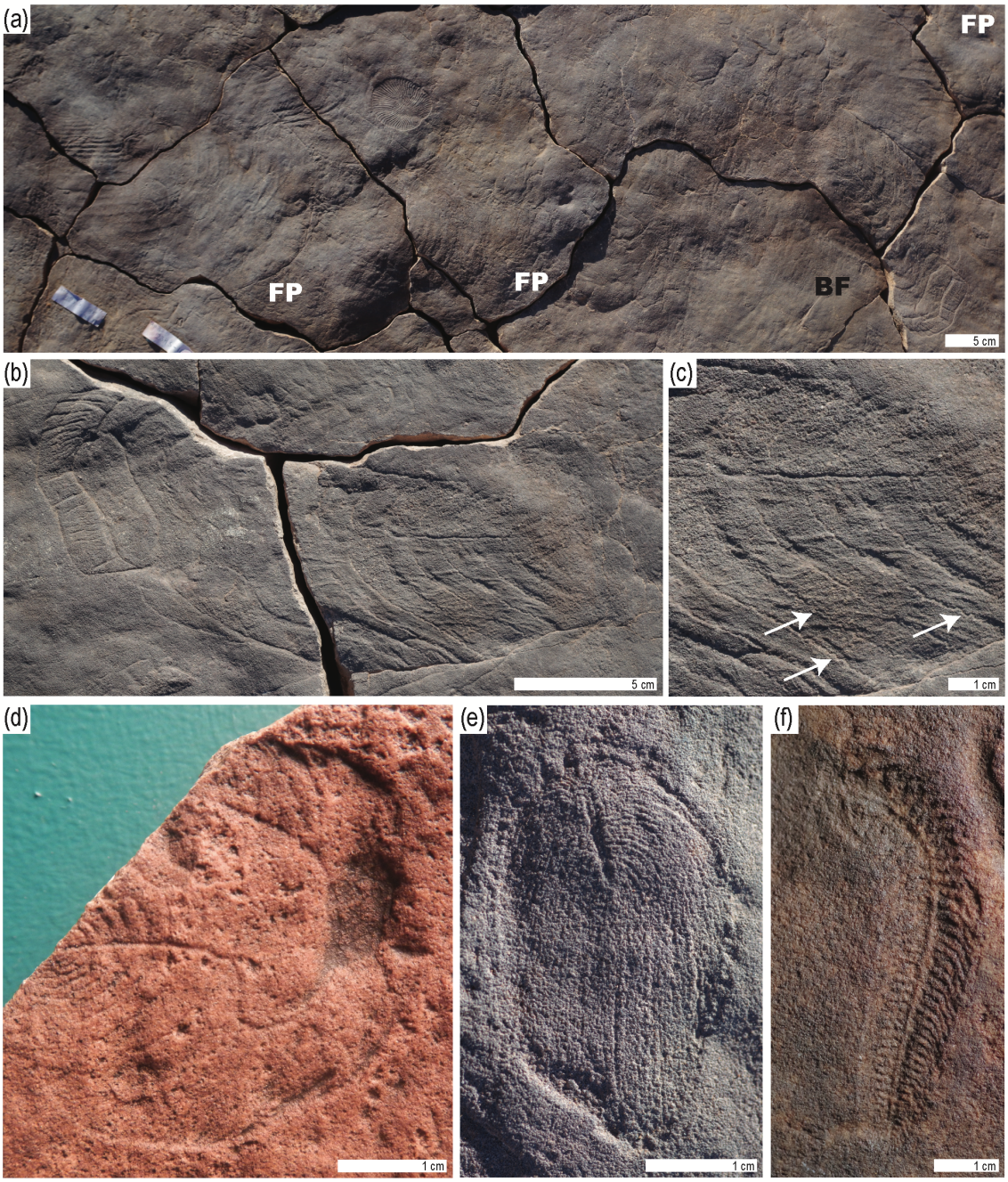
(a)
FP
FP
FP
BF
5 cm
(b)
5 cm
(c)
1 cm
(d)
1 cm
(e)
1 cm
(f)
1 cm

Figure 28. Other potentially mobile Ediacaran taxa, including: a-d) *Yorgia waggoneri* body fossils (BF) and footprints (FP), notice the deep preservation of *Dickinsonia* in the middle of (a), compared with that of the *Yorgia* body fossil in the lower right; e) *Andiva ivantsovi*; and f) curved specimen of *Spriggina floundersi*. a-c) TB-ARB *Yorgia* trackway with body fossil and several footprints, (b) rotated and enlarged view of complete body fossil, and (c) enlarged view of modules from the body fossil with white arrows indicating crooked, zig-zag modules. (a-c) TB-ARB 002. (d) P48132. (e) TB-ARB 003. (f) P12771.

The recent discovery of a body fossil of *Yorgia* on bed TB-ARB (Figure 28a, b) represents the first specimen from an excavated bedding plane surface at Nilpena in association with footprints. The TB-ARB specimen exhibits a highly irregular outer margin (Figure 28b, c), and body fossils of *Yorgia* from the Ediacara Member are typically more variable in outer morphology than those of *Dickinsonia*. Comparison with a closely associated complete footprint suggests that this specimen is contracted to 70% of its original length and less than 50% original width. Body fossil relief is far less than that of significantly smaller *Dickinsonia* from the same bedding plane. Despite finding only one body fossil, there are 27 *Yorgia* footprints on TB-ARB, compared with more than 50 *Dickinsonia* body fossils and 7 *Dickinsonia* footprints.

The TB-ARB specimen suggests that *Yorgia* was much more susceptible to contraction prior to, during or immediately following burial. This contraction may be related to a seemingly more elastic outer integument, potentially filled with a greater volume of fluid, compared with that of *Dickinsonia*. The high abundance of footprints relative to body fossils of *Yorgia* indicates that this organism may have moved more frequently than *Dickinsonia*. However, the typically larger size of *Yorgia* compared with body fossils of *Dickinsonia* increases the likelihood of footprint preservation.

Footprints of other dickinsoniomorphs have not been identified, however similar modular morphology and evidence of body manipulation in *Andiva* (Figure 28e) indicates that they may share the ability to move (Fedonkin, 2002; Evans et al., 2019b). Asymmetrical preservation in the bilateralomorph *Spriggina* suggests body manipulation potentially related to movement (Figure 28f). On bed TC-MM3 the orientation of both the long axis and curvature of *Spriggina* are apparently random with respect to one another and paleocurrent indicators, demonstrating that this was unlikely the result of taphonomic alteration. Seven curved specimens of *Spriggina* occur on bed 1T-F and four occur on bed TB-ARB where there is little evidence of current influence (Evans et al., 2019a). This supports the hypothesis that *Spriggina* was capable of body manipulation, perhaps involving some sort of lateral torsion, which could have resulted in mobility.

Parvancorina, another bilateriomorph, is interpreted to have been mobile in order to orient itself with respect to current. (Paterson et al., 2017; Darroch et al., 2017; Coutts et al., 2018). The lack of discernible trace fossils related to *Andiva*, *Spriggina* or *Parvancorina* indicates that they did not feed in the same manner as other mobile taxa, supporting previous claims for various modes of feeding in Ediacaran organisms (e.g. Rahman et al., 2015; Darroch et al., 2017).

Conclusions

Fossils of the White Sea assemblage definitively record dynamic interactions between four mobile taxa – the progenitor of *Helminthoidichnites*, *Kimberella, Dickinsonia* and *Yorgia* – and the organic mat bound substrate that lined the Ediacaran seafloor. Quantitative and qualitative data reject hypotheses that negative impressions in the mat surface associated with *Dickinsonia* and *Yorgia* represent decayed or passively transported specimens and are consistent with these organisms having been capable of active movement.

Mobility in *Dickinsonia* and *Yorgia* occurred on short, ecologic timescales over distances ranging from a few centimeters to several meters. Impressions left in the organic mat during periods of immobility were almost immediately obscured by regrowth of organic matter following the movement of that organism to a new location. The morphology of *Dickinsonia*, reconstructed based on both body fossils and footprints, indicates that it was bilaterally symmetrical. Rare structures suggest that *Dickinsonia* and *Yorgia* contained at least two competing muscle groups fixed at the midline and outer margin. Mobility was likely achieved by alternating expansion and contraction of these muscles on either side of the midline. The similarity between the magnitude of displacement and size of the organism, discovery of multiple footprints produced by the same individual despite relatively rapid mat regeneration and accurate replication of ventral

morphology demonstrates that footprints formed as the result of active mat removal by *Dickinsonia* and *Yorgia,* likely related to feeding.

Morphological features found in *Andiva* and *Spriggina* suggest that these organisms were also capable of body manipulation, possibly related to mobility. Combined with *Parvancorina*, *Helminthoidichnites,* trace fossils associated with *Kimberella* and evidence for mobility in dickinsoniomorphs, this indicates that many more Ediacara taxa were mobile than classically envisaged (e.g. Seilacher et al., 2003). Further, our results demonstrate that Ediacaran ecosystems were remarkably dynamic, with organisms exhibiting a diversity of life modes and feeding habits (Darrcoh et al., 2017; Droser et al., 2017).

Not surprisingly all of the mobile organisms recognized here were bilaterally symmetrical, indicating that this body organization was advantageous for mobility. Based on the findings reported above, it is likely that other bilaterally symmetrical organisms in the Ediacaran were capable of movement but simply did not leave trace fossils on the mat dominated Ediacaran seafloor. The recognition of multiple disparate bilaterally symmetrical organisms capable of mobility supports previous interpretations that the bilaterian last common ancestor contained at least the developmental capacity for mobility (e.g. Erwin, 2015).

CHAPTER 4: UNEXPECTED STRUCTURAL INTEGRITY COMBINED WITH HIGH EXTENSIBILITY IN THE ICONIC EDIACARA FOSSIL *DICKINSONIA*

Abstract

Dickinsonia is one of the oldest macroscopic metazoans in the fossil record. Determining the biological characters of this extinct taxon is critical to our understanding of the early evolution of life. Preservation of abundant specimens from the Ediacara Member, South Australia, in a variety of taphonomic states allows the unparalleled opportunity to compare the biomechanical responses of *Dickinsonia* tissue to various forces with those typical of modern organisms. *Dickinsonia* are found as lifted, transported, folded, rolled, ripped, and expanded or contracted individuals, while maintaining diagnostic morphology. This suite of characters indicates that *Dickinsonia* was composed of material that was flexible, difficult to rip and capable of elastic and plastic deformation. While none of these traits are diagnostic of a single biomaterial component, we find many similarities with modern biopolymers, particularly collagen, keratin and elastin. Maintenance of significant relief following complete tearing suggests that *Dickinsonia* was composed of relatively thick tissues, signifying higher-oxygen requirements than previously hypothesized. The ability to be transported and still preserve recognizable fossils is unique amongst the Ediacara Biota and demonstrates that *Dickinsonia* was a taphonomic elite. Combined with discovery in multiple environmental settings, this indicates that the absence of *Dickinsonia* represents

the likely extinction of this organism prior to the Nama assemblage, possibly due to a decrease in the global availability of oxygen in the latest Ediacaran.

Introduction

Biomaterial studies have broad implications for fields ranging from evolutionary biology to mechanical engineering (Vogel, 2013). The nature of the paleontological record typically renders such enquiries problematic for extinct organisms. Exceptional preservation of the soft-bodied Ediacara Biota (571-539 Ma) in disparate environments under variable conditions provides the opportunity to examine responses to both external and internal forces and constrain biomechanical properties (Meyer et al., 2014).

The Ediacara Biota represents the oldest fossil communities of macroscopic organisms (Xiao and Laflamme, 2009; Droser and Gehling, 2015). Most taxa are enigmatic, but there is general consensus that among them were members of the major animal clades, including sponges, ctenophores, cnidarians and bilaterians (Erwin et al., 2011). Ediacara taxa are classically divided into three temporally successive assemblages: the Avalon, White Sea, and Nama assemblages (Waggoner, 2003). Diversity loss between the White Sea and Nama assemblages has been recently suggested to represent an extinction event (Darroch et al., 2018; Evans et al., 2018; Muscente et al., 2019).

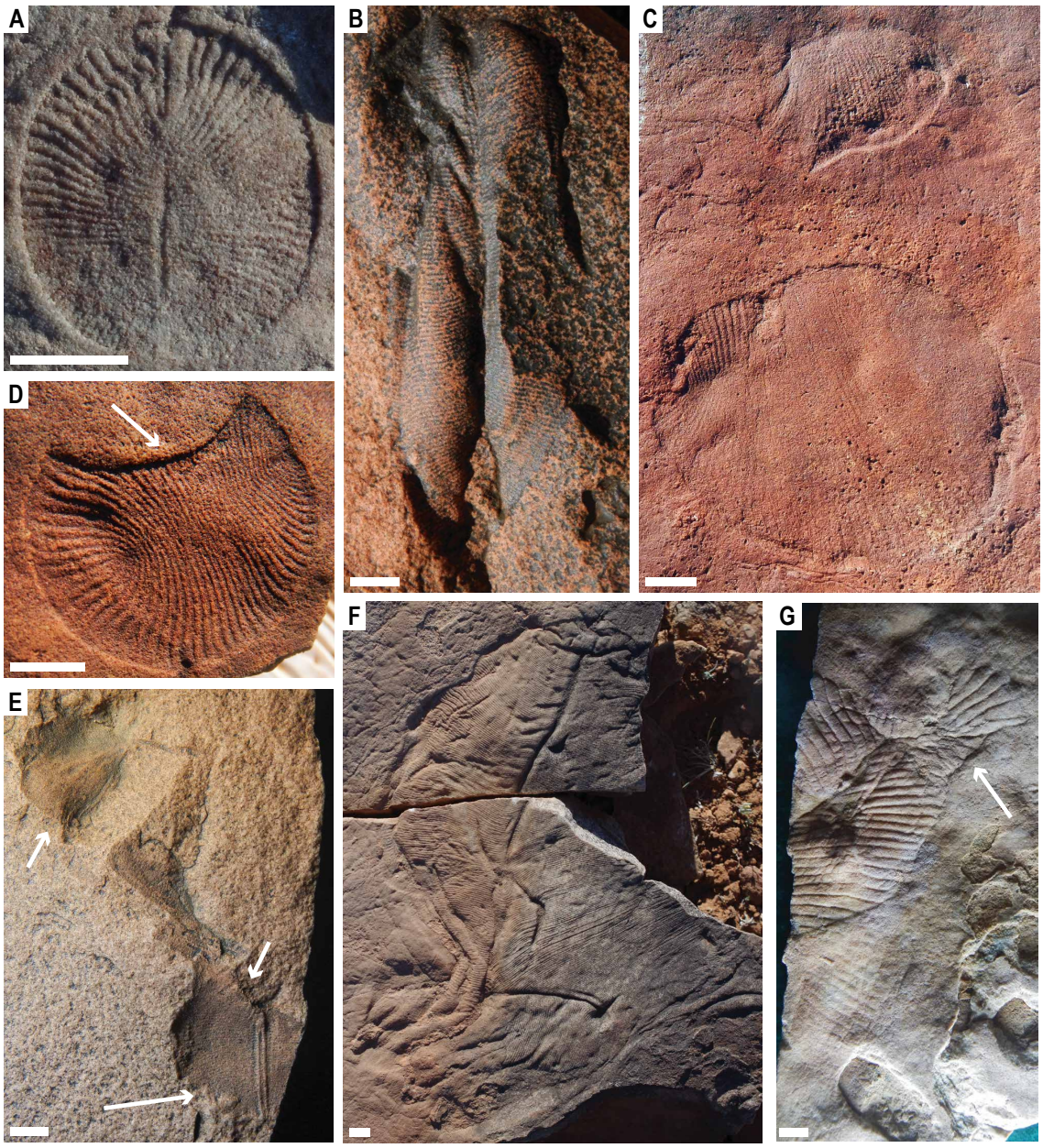
A
B
C
D
E
F
G

Figure 29. Taphonomic variants of *Dickinsonia*, including: (A) classic *Dickinsonia costata* morphology preserved *in situ* in negative hyporelief with modules and midline expressed as negative grooves, indicating greater relief in the original organism; (B) transported, enrolled specimen preserved within a mass-flow deposit from the Ediacara Member (Gehling and Droser, 2013); (C) two stretched, likely transported *D. costata*, see also Figure S1; (D) *in situ* incomplete *Dickinsonia*, with missing morphology (white arrow) partially lifted off of the seafloor; (E) transported, ripped specimen, with blunt and wide-open fracture morphology (white arrows), strong overall negative relief and clear preservation of midline and module boundaries; (F) folded, heavily deformed and likely transported *Dickinsonia rex*; and, (G) twisted, potentially transported *Dickinsonia* (white arrow indicates location of twist) preserving both the top and bottom surface in identical relief. Notice the lack of a midline in C and D. Despite evidence of deformation, all specimens are well preserved, exhibiting clear outer margins, module boundaries, and, when present strong midlines. (A) 1T-F 001; (B) N08-05; (C) TC-MM1 001 (top), 002 (bottom); (D) P49420; (E) P57450; (F) EOS 001; (G) P40927. Scale bars 10 mm.

Dickinsonia, an iconic White Sea assemblage taxon, is an ovoid, modular fossil with a midline down the long axis (Figure 29A; Sprigg, 1949). It is one of few Ediacara Biota taxa with evidence for mobility, musculature and ventral feeding on organic matter (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010; Evans et al., 2019b). While previous phylogenetic interpretations vary dramatically, abundant data now supports classification as a eumetazoan (Gold et al., 2015; Evans et al., 2017; Hoekzema et al., 2017; Bobrovskiy et al., 2018; 2019).

Dickinsonia occurs in all fossiliferous facies of the Ediacara Member (Rawnsley Quartzite) in the Flinders Ranges area of South Australia (Gehling and Droser, 2013). Body fossils are commonly preserved *in situ* on the base of sandstone beds as external molds in negative hyporelief (Gehling, 1999). The midline and module boundaries are typically expressed as ridges with greater negative relief than the rest of the organism, although rarely the midline is found in positive hyporelief.

Several authors have recognized that *Dickinsonia* was capable of expansion/contraction while remaining relatively stiff (Runnegar, 1982; Gehling et al., 2005; Seilacher, 1989; Wade, 1972; Valentine, 1992). Valentine (1992) suggested that it was likely composed of cnidarian mesoglea, a mix of collagen and gel matrix. Alternatively, Retallack (1994) proposed that *Dickinsonia* was

made of chitin. Here we present new data regarding the biomaterial properties of *Dickinsonia* and their implications for the early evolution of animals.

Results

We examined 1,353 body fossils and 130 trace fossils of *Dickinsonia* at the National Heritage Nilpena site (Droser et al., 2019a) and the South Australia Museum. We constrained the typical morphology of *Dickinsonia* using taphonomically unaltered specimens (Figure 29A), allowing the recognition of specimens with atypical morphologies (Figure 29B-F). We examined such specimens to assess how the tissues of *Dickinsonia* responded to various forces.

Previous work demonstrated that *Dickinsonia* was flexible enough to be lifted upward into the water column during storm events (Evans et al., 2015; Bobrovskiy et al., 2019). Specimens transported prior to burial display enrollment (Figure 29B), folding (Figure 29F) and are rarely completely twisted, preserving imprints of both the top and bottom surface (Figure 29G).

The discovery of several clearly transported, completely ripped specimens, with blunt and open fracture morphologies, demonstrates that specimens of *Dickinsonia* could be preserved after exposure to sufficient forces to initiate tearing (Figure 29e; Figure 9 of Gehling et al., 2005). Partially fractured

specimens are not known. Ripped individuals maintain significant relief and diagnostic morphological features, including distinct modules.

Unaltered *Dickinsonia* exhibit a consistent total length to width ratio (Evans et al., 2017) and, typically, equal widths of modules on either side of the midline (Figure 29A). Rare specimens suggest significant, permanent stretching. In one example (Figure 29C, bottom) a single module varies in width (distance from the midline to outer margin) from 32.55 mm to 61.67 mm (Figure 30). Commonly, the midline is absent in both transported (Figure 29C) and *in situ* (Figure 29D) specimens. While these represent permanent states of deformation, the specimens themselves are well-preserved with intact modules.

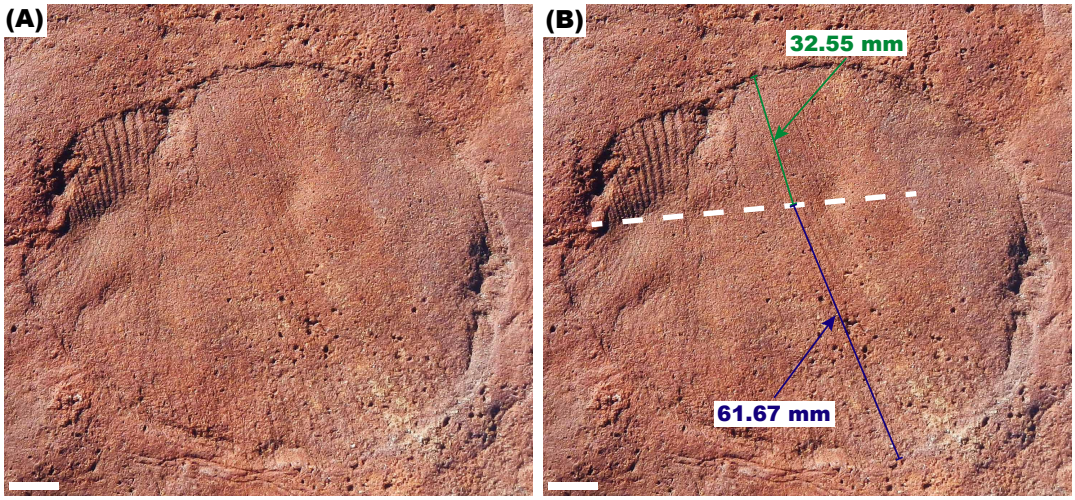

Figure 30. Specimen from Figure 25C (TC-MM1 002) with (a) close up shot of the deformed *Dickinsonia* and, (b) location of midline (dotted white line) and module width measurements (green and purple lines) indicated. Scale bars 10 mm.

Trace fossils of *Dickinsonia* are preserved in positive hyporelief representing the infill of depressions formed by the removal of organic matter lining the Ediacaran seafloor (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Sperling and Vinther, 2010; Evans et al., 2019b). Twelve, associated, complete body and trace fossils (Figure 31A) give accurate estimates of size when creating the trace and at death (Table 3). Of these, 10 trace fossils are larger than related body fossils. The average ratio of trace to body fossil total length is 1.19, with a maximum value of 1.60. We interpret this as evidence of expansion, possibly related to feeding (Sperling and Vinther, 2010; Evans et al., 2019b). *Dickinsonia* trace fossils exhibit identical length to width and total length to midline length ratios as those of body fossils (Figure 32).

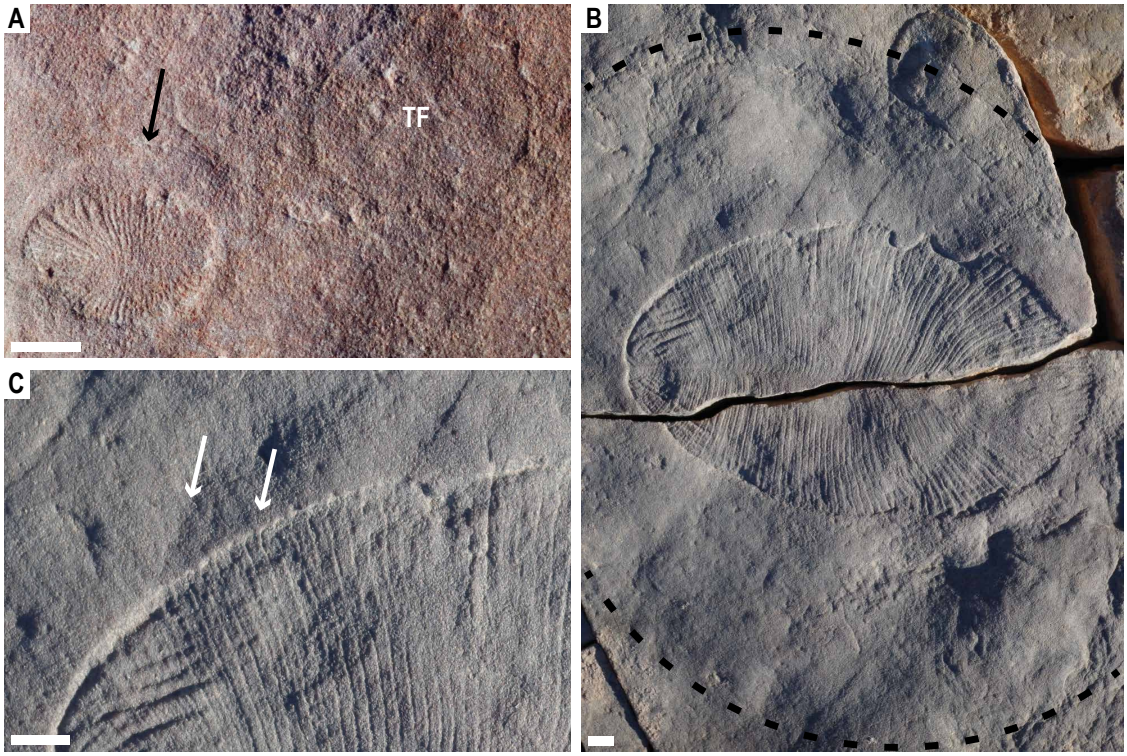

Figure 31. Associated body and trace fossils, demonstrating: (A) body fossil (left) and slight larger trace fossil (right, TF) left by the same organism, notice the slight rim around the body fossil (black arrow), indicating that it is sitting in another trace fossil it created when expanded; and, (B,C) body fossil surrounded by larger trace fossil (black dotted lines indicate extent of trace). (C) Close up of body and trace fossil contact, demonstrating clear continuation of module boundary from body fossil to its signature in the trace fossil (white arrows). (A) MM3 001; (B,C) 1TF 002. Scale bars 10 mm.

Table 3. Comparison of Total Length (TL) between associated Body Fossils (BF) and Trace Fossils (TF). P numbers refer to specimens from the South Australia Museum, all other specimen indicators refer to beds from the Nilpena field site (see Droser et al., 2019a for more information).

Specimen	BF-TL	TF-TL	TF/BF (TL)
P40845	22.163	29.205	1.318
P40860	13.441	12.373	0.921
P40979	33.688	38.193	1.134
P48729	46.689	59.952	1.284
P49377	104.17	102.902	0.988
1T-F 276s 214e	149.566	226.788	1.516
TB-ARB 709s 368e	19.5	21.104	1.082
TB-BRW 631s 426e	67.59	80.777	1.195
TC-MM1 P6	109.283	124.267	1.137
TC-MM3 44s 298e	29.065	32.09	1.104
TC-MM3 57s 216e	35.624	36.043	1.012
TC-MM3 610s 175e	32.16	51.303	1.595
Mean			1.190

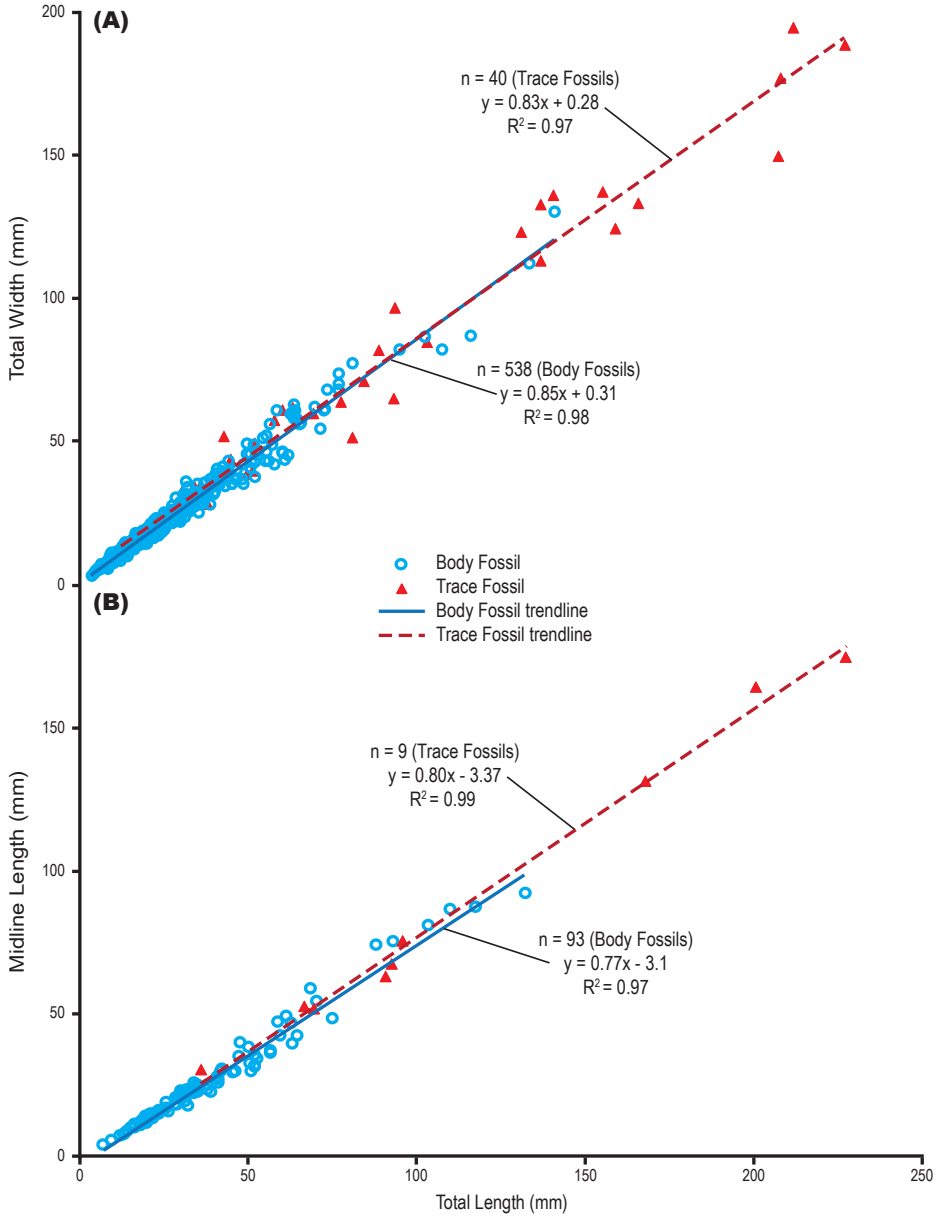

Figure 32. Comparison of body and trace fossil total length, versus (a) total width, and; (b) midline length. Body fossil data from Evans et al., 2017.

Eighteen body fossils are surrounded by larger trace fossils (Figure 31). Module boundaries of body fossils are continuous with surrounding trace fossils (Figure 31C). Modules increase in size, but not number, concurrent with increases in length and width. We interpret these as *Dickinsonia* caught in the act of making the trace fossil. *Dickinsonia* was expanded when creating trace fossil depressions, and, prior to burial, contracted and remained in place. Average trace fossil total length is 1.19 and width is 1.31 times that of associated body fossils (Table 4). Maximum diameter change is observed in a body fossil with a total width of 96.32 mm surrounded by a trace fossil 240.24 mm wide (Figure 31B), representing expansion by a factor of 2.5. Limited evidence of folding cannot account for this large fluctuation in size.

Table 4. Comparison of Total Length (TL) and Total Width (TW) between Body Fossils (BF) and surrounding Trace Fossils (TF). P numbers refer to specimens from the South Australia Museum, all other specimen indicators refer to beds from the Nilpena field site (see Droser et al., 2019a for more information).

Specimen	BF-TL	BF-TW	TF-TL	TF-TW	TF/BF (TL)	TF/BF (TW)
P12776	38.211	36.417	45.912	45.201	1.202	1.241
P14327	125.593	89.274	207.165	152.557	1.649	1.709
P14361	23.991	25.145	28.871	30.331	1.203	1.206
P14370	41.3	38.875	47.165	46.346	1.142	1.192
P35660	74.554	74.071	85.449	82.265	1.146	1.111
P41013	47.948	37.165	55.558	53.313	1.159	1.434
P41086	19.466	16.756	21.812	19.366	1.121	1.156
P41093	15.72	16.327	17.37	19.125	1.105	1.171
P41197	37.56	33.904	43.361	38.22	1.154	1.127
P47756	35.465	25.668	38.808	31.443	1.094	1.225
P47824	87.964	56.893	98.569	75.854	1.121	1.333
P49282	30.193	26.153	34.86	29.558	1.155	1.130
P49377	97.866	80.382	107.204	92.846	1.095	1.155
1T-F 001	34.411	31.441	37.461	36.749	1.089	1.169
1T-F 002	151.811	96.319	212.252	240.24	1.398	2.494
N08-04	29.063	24.259	33.102	27.977	1.139	1.153
N11-14	23.029	20.455	24.841	23.761	1.079	1.162
TC-MM3 001	28.884	21.651	36.927	31.593	1.278	1.459
Mean					1.185	1.313

Extensibility, the extent to which a material can be stretched before fracture occurs, is calculated as the natural log of expanded length before failure divided by original length (Vogel, 2013). Permanently stretched individuals and associated body and trace fossils allow minimum estimates of extensibility. In both examples, we find evidence supporting previous claims that *Dickinsonia* could expand to more than twice its original length (Wade, 1972; Runnegar, 1982), indicating extensibility greater than 0.7.

Discussion

The discovery of recognizable *Dickinsonia* after transport suggests that it was relatively resilient for a soft-bodied organism. Observed responses to applied forces, including torsion (enrolled and folded specimens) and tension (stretched specimens), indicate high flexibility. Several modern biopolymers, including collagen-containing composites in sea anemone mesoglea, keratin in hagfish slime thread, and elastin fibers in arteries allow comparable flexibility and shape change (Koehl, 1976; Shadwick, 1999; Fudge et al., 2003).

Variable relief indicates that *Dickinsonia* modules and module boundaries had slightly different properties. Variable collagen content and fiber orientation in distinct portions of mussel byssal thread provides regio-specific extensibility, allowing firm attachment to substrates experiencing high-energy wave activity (Bell and Gosline, 1996). Combining crystalline and amorphous keratin, such as

in wool, yields biopolymers with both stiffness and extensibility (Fuegheman, 1997; Huang et al., 2019) analogous to the differential properties of modules and their boundaries.

Bobrovskiy et al. (2019) suggested that the top of *Dickinsonia* was preserved because it was more resilient. Specimens with the top and bottom of the organism in equal relief (Figure 29G) do not support such differences (Ivantsov, 2019). Rare specimens lacking a midline or with a midline preserved in positive relief indicate differential responses to deformation. The maintenance of a constant midline to total length ratio in expanded and contracted individuals suggests minor compositional dissimilarities.

The prominent relief of ripped *Dickinsonia* indicates relatively thick tissues, strong enough to resist compaction. Dehydration/deflation of the organism was minimal even following complete rupture. Interestingly, the fractured morphology of *Dickinsonia* is blunt and wide open (Figure 29E, white arrows), distinct from commonly observed crack initiation and propagation in materials such as bones and chitinous exoskeletons (Ritchie, 2011; Weaver et al., 2012). Such behavior is found, for example, in hydrated skin, where tears do not tend to propagate, but rather open and blunt under tensile loading, due to the reorientation and stretching of collagen fibers (Yang et al., 2015).

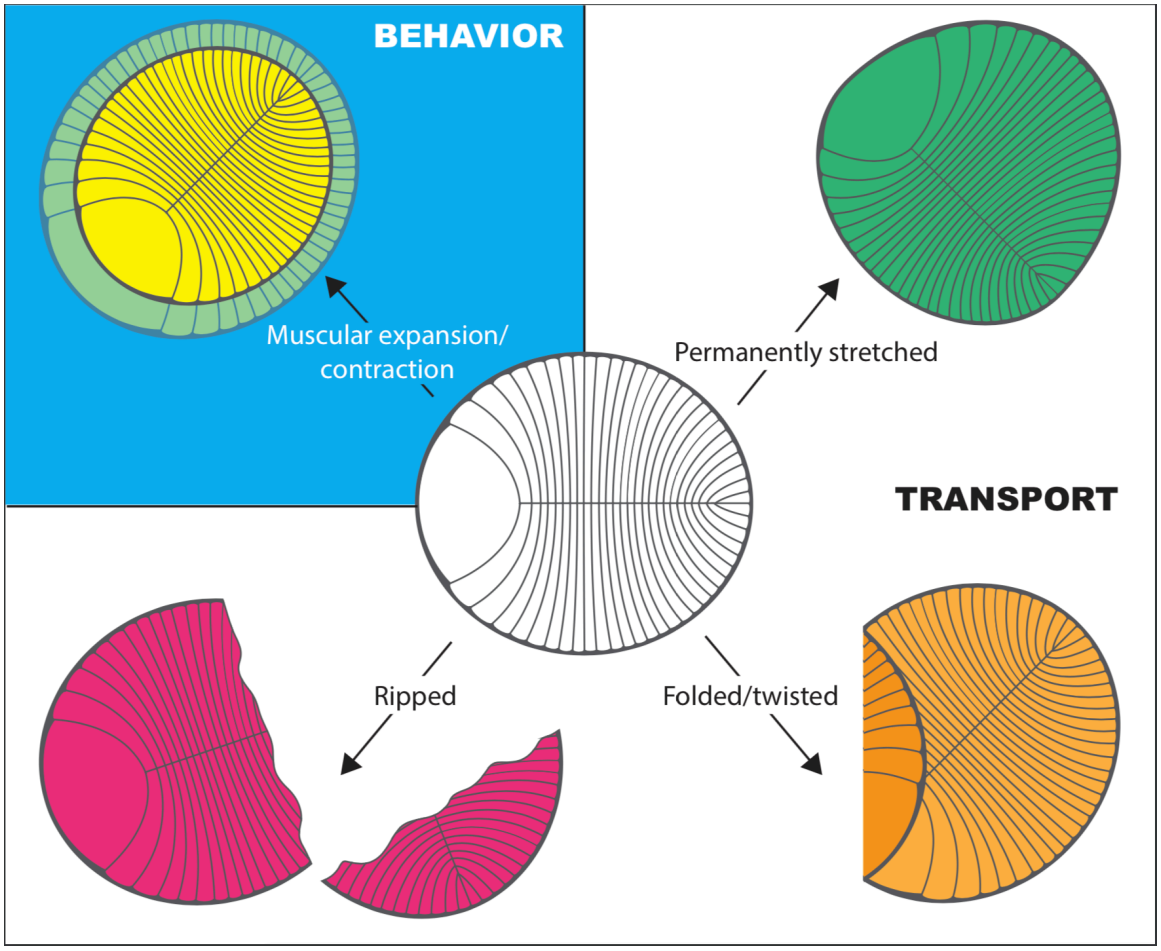

Figure 33. Variable responses of *Dickinsonia* tissue to forces, including both those exerted on the organism through its own activity (behavioral) and those imparted from the external environment (transport).

The combination of observed elastic (return to original shape) and plastic (permanent) deformation indicates variable responses of *Dickinsonia* tissue to different forces (Figure 33). Plastic deformation could be attributed to death prior to burial, however exceptional preservation suggests a lack of exposure necessary to produce recognizable decay. Thus, although the organism likely

died as a result of these forces, we interpret the deformation to accurately reflect the mechanical properties of living *Dickinsonia* tissue. These traits provided the rigidity necessary to maintain diagnostic morphology, while rarely producing the appearance of plastic deformation when exposed to high-velocity, turbulent forces during transport.

The ability to calculate minimum estimates of extensibility for *Dickinsonia* allows direct comparisons with modern biopolymers. Observed values are relatively high compared with most materials (Vogel, 2013). Sea anemone mesoglea and mussel byssal threads, both collagen composites, exhibit similar extensibility (Wainwright et al., 1976; Koehl, 1977). Values in chitin composites range from 0.01 in arthropod cuticle to 16 in the intersegmental membranes of pregnant locusts (Vincent, 1975; Vogel, 2013). Rubbers produced from proteins in animals, such as elastin, keratin and abductin, exhibit extensibility values of approximately 1, although these do not typically produce materials as resilient as is inferred for *Dickinsonia* (Vogel, 2013).

Collagen is one of the most resilient biomaterials; it is remarkably efficient at storing energy (Wainwright et al., 1976). This would have been highly beneficial for the peristaltic mobility of *Dickinsonia* (Evans et al., 2019b). Further, many invertebrates today, from sea anemones to annelids, use collagen composites to build body walls with high extensibility (Elder, 1973; Koehl, 1977). Such tissue is

commonly paired with muscular motility, as is interpreted for *Dickinsonia*, for example in sea cucumbers that burrow via peristalsis (Alexander, 1962). Protein rubbers are also capable of storing and releasing energy, albeit at slightly less efficient levels than collagen, and are used in conjunction with muscular activity (Elder, 1973; Vogel, 2013).

Pteridinium from Ediacaran deposits in Namibia have been similarly interpreted as rigid yet flexible and likely composed of collagen, chitin and/or cellulose (Meyer et al., 2014). Both collagen and chitin have been identified in fossil taxa from the Cambrian (Parsley and Prokop, 2004; Ehrlich et al., 2013). The ubiquity of such materials in modern organisms (Vogel, 2013) further indicates that Ediacara taxa, including *Dickinsonia*, would have had the developmental capacity to produce these biopolymers.

Implications

Elastic and plastic deformation in *Dickinsonia*, along with comparable extensibility, fracture mechanisms, high-energy storage and flexibility are most parsimonious with the properties of collagen and gel composites. However, other biopolymers, such as keratin and elastin, cannot be ruled out. Collagen is the most abundant protein in modern metazoans (Baccetti, 1985; Exposito et al., 2010), so it is not surprising that Ediacaran aged animals produced this biopolymer. The compositional variability observed here between the midline,

modules and module boundaries may indicate the evolution of disparate fibrillar collagen clades, hypothesized to have occurred prior to the eumetazoan radiation (e.g. Exposito et al., 2010). Regardless, tissue differentiation is evidence of eumetazoan-grade complexity in *Dickinsonia*.

Nama-aged fossils from Namibia have been recognized in facies comparable to those from the Ediacara member (Darroch et al., 2015). *Dickinsonia* has been identified in all four fossiliferous facies of the Ediacara Member, including those containing Nama assemblage taxa (Droser and Gehling, 2013). This suggests that if *Dickinsonia* was present during the latest Ediacaran we could reasonably expect to find fossil evidence alongside the Nama assemblage. Thus, we interpret the lack of *Dickinsonia* in these deposits to be a meaningful absence, rather than a taphonomic artefact. This is consistent with the likely extinction of *Dickinsonia* before the latest Ediacaran (Darroch et al., 2018).

It has been hypothesized that *Dickinsonia* and other similar taxa reduced their oxygen requirements by limiting tissue thickness (Sperling et al., 2015). This would maintain virtually all cells in contact with seawater, allowing tolerance of lower oxygen conditions (Alexander, 1971; Payne et al., 2011). Here we demonstrate that *Dickinsonia* tissues were much thicker than that theoretical minimum. Evidence for musculature and extensive mobility (Gehling et al., 2005; Evans et al., 2019b) further suggests that the oxygen demands of *Dickinsonia*

were high compared to contemporaneous sessile taxa composed of thin tissues. Combined with evidence for decreasing global oxygen availability in the late Ediacaran (Evans et al., 2018; Zhou et al., 2018; Tostevin et al., 2019) these results support interpretations that environmental disturbance led to the first extinction in the fossil record.

CONCLUSION

The Ediacara Biota records the critical transition from simple, microscopic organisms to the diversity of macroscopic life that exists today. While some of these forms can be reliably attributed to modern phylogenetic groups, a number have uncertain affinities. The chapters presented above demonstrate the utility of quantitative evaluations of Ediacara Biota fossils focused on their biological and ecological traits in order to understand where they fit in the elocutionary history of life on Earth.

To that end, identifying variations, or lack thereof, between different preservational conditions within the Ediacara Member provides the necessary background to determine when these characters are meaningful and rule out those due to taphonomy. Recognizing that the organic mat was difficult to penetrate is critical in assessing potential mobility in Ediacaran taxa. Without the preservation of resilient taxa in various states of deformation, we would not be able to recognize the biomechanical responses of certain tissues to various forces. A holistic view of the Ediacara Biota, presented in their environmental and taphonomic context, is essential to understanding these organisms.

Within that context, well-preserved specimens indicate that *Dickinsonia* grew in a highly-regulated, complex manner, was bilaterally symmetrical, mobile, contained muscles, and had differentiated tissue. These characters are consistent with

those expressed in bilaterians today. However, the identification of feeding through the entirety of the ventral surface and lack of morphological evidence for any type of body opening(s) suggest that *Dickinsonia* lacked a mouth, anus or through-gut. Predictions based on gene sequencing of modern metazoans (e.g. Erwin and Davidson, 2002) suggest that the Ediacaran should contain lineages utilizing gene regulatory networks common to all animals but that did not give rise to modern groups. Together, the characters of *Dickinsonia*, and related forms such as *Yorgia,* indicate that they may represent such extinct lineages.

Despite the large focus of this work on a single genus, it also highlights the diversity of successful organisms within the Ediacara Biota. *Dickinsonia, Yorgia* and *Andiva* are all considered dickinsoniomorphs, sharing the same basic body construction, yet it is clear that distinct taxa had variable growth patterns. All three were likely mobile but displayed different proportions of trace fossils relative to body fossils, and likely manipulated their bodies to different extents, possibly due to variations in their biomaterial composition. While *Dickinsonia* and *Yorgia* appear to have obtained nutrients through their entire ventral surface, *Andiva* may not have, and many other Ediacaran taxa did not.

As with many extinct fossil taxa, members of the Ediacara Biota are often viewed as “failed experiments”, however, they were remarkably successful for millions of years. Importantly, they evolved in a context far different from those typical of

modern day, shallow marine ecosystems, and their enigmatic nature likely reflects such conditions. While particular adaptations allowed these organisms to thrive, changing environmental conditions apparently had major impacts on the lifestyle of these organisms, and as a result many may have gone extinct prior to the onset of the Cambrian.

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